Breeding and development of the endangered Purple-spotted Gudgeon *Mogurnda adspersa* population from the Murray Darling

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ABSTRACT

The Purple-spotted Gudgeon, *Mogurnda adspersa*, is widespread occurring in coastal drainages in northern NSW and Queensland, and an endangered western population in the Murray Darling System. This paper reports a study at the Inland Fisheries Research Station, Narrandera in the 1960s using fish from the western population. *M. adspersa* bred in ponds and aquaria at temperatures between 20.0 and 29.9°C (34.0°C at water surface), and in ponds between December and February. An abundant food supply was essential but rising water levels were not required. The elaborate spawning behaviour and embryological development of the eggs, larvae and juvenile fish were recorded. The eggs were demersal, transparent, telolecithal and elliptical, and they possessed an adhesive disc at one of the pointed ends, although the chorion was essentially non-adhesive. They measured 1.07 - 1.33mm by 2.03 - 3.78mm, and were attached in a cluster to solid objects. Their oil globules were small and numerous. The eggs hatched 3 – 8d after fertilisation, at temperatures of 20.2 - 29.0°C. The length of larvae at hatching varied from 3.44 - 4.15mm. The prolarval stage terminated approximately 6½d after hatching at temperatures between 19.0 and 29.0°C, when the larvae measured 5.30 - 5.85mm in length. Opercular stripes appeared on juveniles between 12 and 20mm in length, and males and females were mature at 44.7 and 49.0mm respectively. Adult males often had a pronounced bulge on top of the head. The longest fish from the western population was 99.0mm. Fecundity varied from 284 to 1300 eggs. The gonosomatic index of females and males ranged from 1.26 - 11.74 and 0.18 - 2.16 respectively. The mean length of fish reared in an aquarium measured 33.0 and 50.0mm at one and two years old, respectively. Eggs, larvae, and breeding biology are compared with other Murray Darling species. The breeding biology of *Mogurnda* species in Australia is discussed which emphasises the taxonomic confusion.

Key words: *Mogurnda adspersa,* Purple-spotted Gudgeon, western endangered population of Purple-spotted Gudgeon, breeding biology, egg and larval development, fishes of inland NSW.

Introduction

Mogurnda adspersa, the Purple-spotted Gudgeon, also known as the Southern Purple-striped Gudgeon, Chequered Gudgeon, Trout Gudgeon, Koerin and Kurrin, was placed in the family Gobiidae, subfamily Eleotrinae by Greenwood *et al.* (1966), but now it has been placed in the Family Eleotridae (Allen and Jenkins 1999; Allen *et al.* 2002; Pusey *et al.* 2004).

In the 1960s and 70s there was uncertainty as to the identity of this species as exemplified by Lake (1966, 1971 and 1978) describing the Murray Darling population as *Mogurnda striata*, *M. adspersa* and *Mogurnda mogurnda* respectively. *M. striata* (Steindachner 1866) was described from specimens from Port Jackson (Sydney?), *M. adspersa* (Castelnau 1878) from the Fitzroy River, Rockhampton, Q and *M. mogurnda* (Richardson 1844) from Port Essington, Northern Territory. It was considered important to use the correct identity but attempts at the time to sort this out were unsuccessful.

Because of this taxonomic confusion and the source of fish not being identified in many early breeding reports, it is important to identify the location of populations being studied and delineate the distribution of *Morgurnda* species. Early reports on breeding may even be related to newly described species. Allen and Jenkins (1999) have recently reviewed the freshwater Australian *Mogurnda* sp., sorted out most of the taxonomy and described four new Australian species.

M. adspersa is one of the six species of *Mogurnda* currently recognised in Australia by Allen and Jenkins (1999) (Fig. 1). *Mogurnda oligolepis* is restricted to the Kimberley region, *Mogurnda larapintae* (Zietz 1896) to the Finke River in central Australia, *Mogurnda thermophila* to the Dalhousie Springs area in South Australia and *Mogurnda clivicola* to the northern end of the Flinders Ranges. Two records (one from author and one from Allen *et al.* 2002)) from the Bulloo overflow along the NSW /Queensland border area could belong to the latter species. The remaining two species have wider distributions, *M. mogurnda* stretching from Darwin to the Cape York Peninsula and *M. adspersa* from the Murray Darling and also in coastal rivers and streams from the Clarence River in northern New South Wales to northern Queensland. *M adspersa* probably overlaps with *M. mogurnda* at the northern part of its range (Pusey *et al.* 2004, Fig.1). In inland south eastern Australia *M. adspersa* used to be distributed in the Lachlan, Murrumbidgee, Murray and

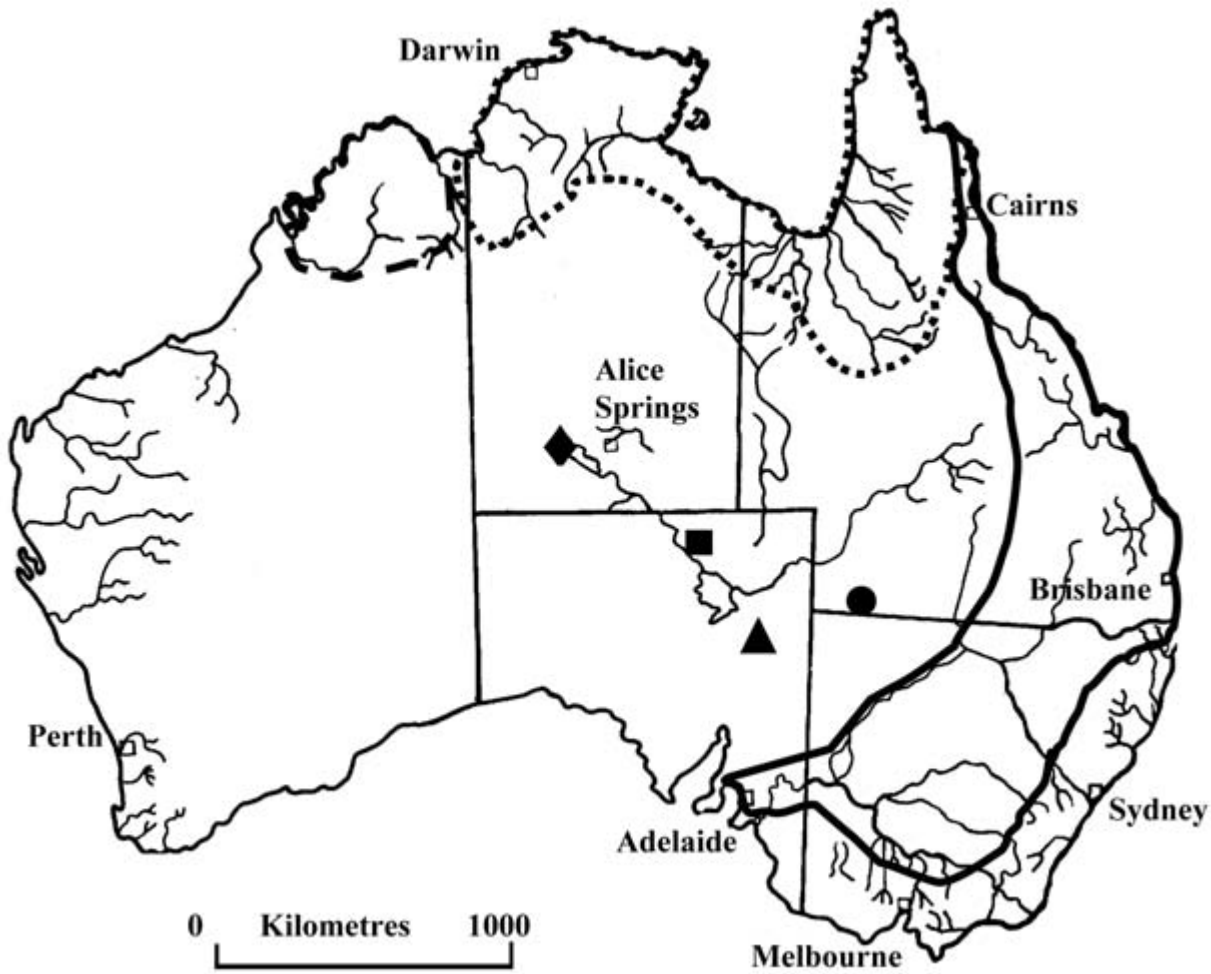


Figure 1. Distribution of *Mogurnda* sp. in Australia based on Allen *et al.* 2002, records of the Australian Museum and authors records. ——— perimeter of range of *M. adspersa*; ▪▪▪▪▪▪▪▪ perimeter of range of *Mogurnda mogurnda;* — — — perimeter of range of *Mogurnda oligolepis* Kimberley region; ▲ = *Mogurnda clivicola* northern Flinders Ranges; ● =Possibly *M. clivicola* but unconfirmed, one specimen taken north of NSW border and one south of the border; ♦ = *Mogurnda larapintae* Finke River MacDonnell Ranges; ■ = *Mogurnda thermophila* Dalhousie Springs.

Torrens Rivers (Blewett 1929) near Adelaide and the upper reaches of the Darling River. The most western record is from Moonta, Yorke Peninsula. Zietz (1902) recorded the Torrens and Onkaparinga Rivers *Mogurnda* as "*M. mogurnda*". In recent years *M. adspersa* has been recorded only from the Cardross Lakes near Mildura (Raadik and Harrington 1996), Deadman's Creek near Tenterfield (Briggs 1998) and a few isolated populations in the headwaters of the Darling (Lintermans 2003).

The inland western population of *M. adspersa* is generally patchy in distribution, uncommon and is seldom found in large numbers. It appears to frequent slow-flowing, non turbid, weedy bodies of water such as irrigation channels, swampy areas where there is plenty of cover, or the weedy margins of the larger and slower flowing rivers. Even within this general habitat type, its presence still appears to be very irregular and there seems little evidence to suggest it disperses a great deal from its preferred habitat, although Whitley (1972) recorded this species in Victoria Park (Brisbane, Queensland) originating from a rain of fish during a thunderstorm. Since recent records are few in the Murray Darling, it is believed that numbers have seriously declined (Briggs 1998, Wager and Jackson 1993), and the "Action Plan Status" of *M. adspersa* (Murray Darling stock) was "endangered" in the "Action Plan for Australian Freshwater Fishes" (Wager and Jackson 1993). In New South Wales, the western population (ie Murray Darling population) of the Purple-spotted Gudgeon (*M. adspersa*) is listed as an "Endangered population" (NSW Fisheries 2004).

The current paper describes the spawning and egg and larval development of the Murray Darling population of *M. adspersa* bred in ponds and in aquaria between 1965 and 1969. Although organogenesis of this fish is similar to that of many other teleosts as depicted by Kuntz and Radcliffe (1915), Lagler (1956), Manner (1964) and many other authors, a detailed description is necessary because the comparative size, shape, and timing of appearance of various organs are the only clues to the identity of egg and larval stages of different species (May and Gasaway 1967). Accurate identification of eggs and larval forms is important for establishment of the presence and success of breeding of this rare species.

Materials and Methods

Reference to *M. adspersa* in this document refers to the Murray Darling population unless otherwise stated. *M. adspersa* was first collected in March 1965 below Willow Dam which is adjacent to Barren Box Swamp, (34°11'S and 145°50'E), and situated 22 km west-north-west of Griffith, in the Riverina district of New South Wales. The abundance of fish in this area was sufficient to support a sampling programme, which also supplied fish for breeding trials.

Samples were obtained up to fortnightly as the breeding season approached from early November and less frequently during winter and at other times of the year. The methods of sampling are identical to those described for *Nannoperca australis*, the Southern Pygmy Perch (Llewellyn 1974). Collections were taken over a 6 hour period during the hours of daylight. Fish were transported 90km to the Inland Fisheries Research Station at Narrandera, in open top 44 gallon drums ½ filled with water.

Fish were kept in artificial ponds and aquaria. Although pond stocking commenced in March 1965, successful breeding in ponds was not detected until December 1967 - February 1968, when only larvae were recovered. Because it was difficult to collect eggs from ponds, despite regular sampling, effort was concentrated on breeding the fish in aquaria where eggs and larvae could be more easily observed and collected. The first successful spawning in an aquarium occurred on 11 February 1968. Twenty two additional spawnings were induced and recorded over the following three years.

Pond trials

The first group of fish to be captured (March, 1965), 39 in all (Table 1), were put into a pond 0.011 ha in area and 1.37 m deep. Regular plankton samples were taken from the pond to capture larvae to determine whether spawning had occurred. Pond temperatures were recorded regularly throughout all breeding trials. A second stocking of 134 fish was carried out between March and December 1967, and samples of adult females were taken between September and December to examine the development of their ovaries. Plankton samples, benthic samples and scrapes from solid objects were carried out regularly from September onwards. The pond was covered with netting to prevent predation by birds and water was run through it from 17 to 26 January 1968. A third slightly larger pond 0.013 ha in area and 1.37 m deep was stocked with 86 fish between 18 December 1967 and 18 January 1968. Routine sampling was carried out but water was not circulated through this pond.

Table 1. Collections of *M. adspersa* at Willow Dam from 1965 – 1970

Date	Water Temperature °C	Numbers	Comment
14.iii.65	-	24	-
23.iii.65	-	15	-
14.iii.66	-	0	-
18.x.66	19.4	20	-
25.x.66	21.0	4	-
2.xi.66	-	60	-
28.ii.67	-	0	-
7.iii.67	21.7	40	-
3.v.67	-	16	-
25.v.67	9.3 – 9.7	1	Juvenile caught in channel among weeds
27.vii.67	6.9 – 12.8	3	Caught in ports, no weeds pH 6.9 – 8.4
4.ix.67	6.9 – 13.0	3	-
18.ix.67	14.7 – 15.0	0	pH 8.3
24.ix.67	15.6	0	-
2.xi.67	21.7 – 24.4	89	Ovaries well developed. 57mm long. Redfin abundant.
23.xi.67	20.6 – 22.8	84	Length 54 – 64mm. Redfin abundant
12.xii.67	21.2 – 24.0	20	Length 44.7 – 62.5mm. Redfin abundant
26.xii.67	-	0	Redfin abundant
18.i.68	22.0 – 28.0	14	-
14.ii.68	23.9 – 26.3	13	pH9.2. Redfin abundant
30.iv.68	-	0	-
4.vi.68	-	0	-
20.vi.68	-	1	31.5mm long, previous summer breeding
30.vi.68	-	0	-
17.ii.70	25.0	0	-
Total (25 visits)		407	

Sampling effort was intensified when the state of the ovaries indicated that spawning was approaching. Plankton nets (0.5mm mesh) were used to collect larvae. Benthic samples were collected by sweeping lightly over the bottom of the pond and scraping from solid objects using a dip net (0.5mm mesh). These samples were sifted through 1.63, 0.53 and 0.25 mm mesh sieves to facilitate examination. The sub samples were examined on a white tray marked with parallel lines spaced slightly less than the field of view of a long rackwork arm microscope.

Aquaria breeding trials

Aquaria trials started in late 1966 in order to obtain eggs and larvae so that their development and spawning could be followed. Aquaria were filled with 90L of water and were stocked with between 3 and 24 adult fish of unknown sex. The aquaria were planted with aquatic plants and aerated, and the adult fish were fed mainly on whole or chopped earthworms, mosquito fish (*Gambusia holbrooki*) and occasionally dragonfly larvae, back swimmers and shrimps. The fish were regularly observed for signs of courtship display and the aquaria were examined daily for signs of nest formation or egg deposition. On a number of occasions during cooler months the aquaria were artificially heated in an attempt to induce spawning. Aquarium temperatures were recorded frequently during the spawning period and occasionally at other times. The pH in aquaria was checked occasionally. Once spawning was successful, further inductions of spawning were attempted by varying conditions of temperature, food supply (abundance and type), cover, time of year etc. in an attempt to find out what were the critical conditions necessary for breeding. These findings were related to field observations.

Pre-spawning and spawning behaviour was observed and recorded in detail including the frequency and duration of spawning, the rate of ovum deposition and numbers of ova deposited.

Newly laid eggs were collected from solid surfaces in aquaria using a scalpel, placed in covered petri-dishes and photographed at regular intervals using normal light microscopy. The particular egg used and the timing of each photograph was noted to assist with later ageing. On occasions photographs were taken using phase contrast microscopy, from which photo composites were made. The development of these eggs and later the larvae were followed in detail. The water temperature in the petri dishes, which was ambient, was recorded. To immobilise larvae for photographing, a drop of quinaldine that could be suspended on a needle tip was added to the Petri dish. Larvae recovered in about 10 minutes. Regular sketches were made of the various developmental stages so that dimensions and timing could be recorded. Newly hatched larvae were kept in an aquarium and measured every 3 months until they were nearly 3 years old. The young fish were fed on finely chopped worms, fine plankton and material from the benthic samples.

Occasional adult specimens were killed, and together with any mortalities were used for the examination of weight and state of maturation of the gonads. These measurements allowed determination of the onset of spawning, using methods similar to those used by Bodola (1964). The universal scale of maturation outlined by Nikolsky (1963) was used to identify the stages of gonadal development. Ovaries that were mature enough to carry out ova counts were preserved in Bouin fixative for a lengthy period until the ova were hard and thus easy to tease apart, and then transferred to 5% formalin. Egg counts were determined gravimetrically. From the weights of fish and gonads the gonosomatic index (G.S.I.) (Mackay 1973) was calculated (G.S.I. = wt. of gonad x 100/wt. of body including gonads). G.S.I is equivalent to the "maturity index" used by Blackett (1968) and the "gonado-somatic index" of Belsare (1962).

Details of the differences between adult male and female fish were recorded but these characters could only be used reliably for sex separation when the spawning period approached.

Results

Induced Breeding

Pond trials

Attempts to induce spawning were governed by the availability of fish from Willow Dam (Table 1). In the March 1965 pond trial only 23 of the 39 fish stocked were retrieved after 18 months. No young fish were found, suggesting breeding had not occurred. In the second trial involving 134 stocked fish by December 1967, examination of ovaries of females indicated they were approaching spawning condition at that time. The first larvae (estimated age 5 days) were recovered from a plankton sample on 31 January 1968, shortly after the flow of water through the pond was stopped (see Table 2). The larvae measured between 5.28 and 5.71mm in length (Mn 5.47mm, n=8). The pond temperatures at the time of larva collection were 34.0^{o}C at the surface and 26.0^{o}C at the bottom (Fig. 2a), and were 31.3^{o}C at 50mm, 27.0^{o}C at 230mm, and the air temperature was 45.0^{o}C. The pond temperatures over the spawning period are shown in Fig. 2a, with surface temperatures at the estimated time of spawning on 21 January 1968 reaching 28.6^{o}C. No ova were recovered and no larvae or young fish were found in the pond when it was finally emptied in March 1968.

In a third trial, involving 86 fish stocked by 18 January 1968, advanced larvae were recovered from plankton samples two weeks later, when pond temperatures were 32.0^{o}C at the surface and 28.8^{o}C at the bottom. The length of larvae collected from this pond on 14 February 1968 indicated that a number of spawnings had occurred (Table 2). When the pond was emptied in June 1968 100 + juveniles were recovered. The pond had a heavy growth of aquatic pond weeds which had probably enhanced fish survival, unlike the other ponds in which losses were experienced.

Since regular sampling had failed to locate eggs in ponds, efforts to induce spawning in aquaria were intensified. *Mogurnda* spp. had been bred in aquaria prior to 1965 (Blewett 1929; Freund 1918; Funnell 1937; Gale 1914, 1918; Hamlyn-Harris 1931; Lederer 1935; Marherr 1937; Schiessl 1937). No further attempts were made to induce breeding in ponds.

Table 2. Successful breeding of *M. adspersa* occurred on all the dates shown.

Date	Time	Location	Water Temperature °C at spawning	Comment
~21.i.68, larvae found 31.i.68	12.00	Pond	Surface 34.0 Bottom 26.0	Larval length 5.20 – 5.71mm (n=8)
Between 12.xii.67-1.ii.68	-	Pond	1.ii.68 Surface 32.0 Bottom 28.8	Larvae found
8.ii.68	12.15	Pond	Bottom 24.2	-
9.ii.68 – 11.ii.68	-	Pond	Bottom 28.9	-
11.ii.68	-	Pond	-	Larvae found
10.ii.68 eggs found 11.ii.68	15.30	Aquarium	Bottom 28.9 Surface 29.0	Eggs first observed 500 laid (13 died)
6.xii.68	-	Aquarium	-	Larvae kept for growth curve
21.iii.69	14.02	Aquarium	29.9	Aquarium heated, 774 ova
30.iv.69	8.0	Aquarium	24.5	-
19.viii.69	-	Aquarium	-	-
22.viii.69	12.10	Aquarium	22.4	Adult fish removed
11.x.69	15.00	Aquarium	-	-
12.x.69	14.30	Aquarium	20.6	-)
14.x.69	8.00	Aquarium	23.4	)
14.x.69	10.30	Aquarium	23.4	)
14.x.69	14.30	Aquarium	20.6	)
15.x.69	17.15	Aquarium	-	) same
19.x.69	12.30	Aquarium	19.2	) aquarium
23.x.69	14.00	Aquarium	20.0	)
24.x.69	-	Aquarium	21.1	)
25.x.69	-	Aquarium	-	Bred twice)
30.x,69	8.30	Aquarium	-	)
6.xi.69	8.15	Aquarium	25.6	)
17.iii.70	-	-	24.7	
10.xi.70	-	Aquarium	24.2	
20.xi.70	-	Aquarium	21.3	
11.xi.71	-	Aquarium	-	100 fry hatched
16.xi.71	-	Aquarium	24.3	Fish kept in aquaria from hatching for growth curves
19.xi.71	-	Aquarium	-	138 eggs laid
27.xi.71	-	Aquarium	-	-

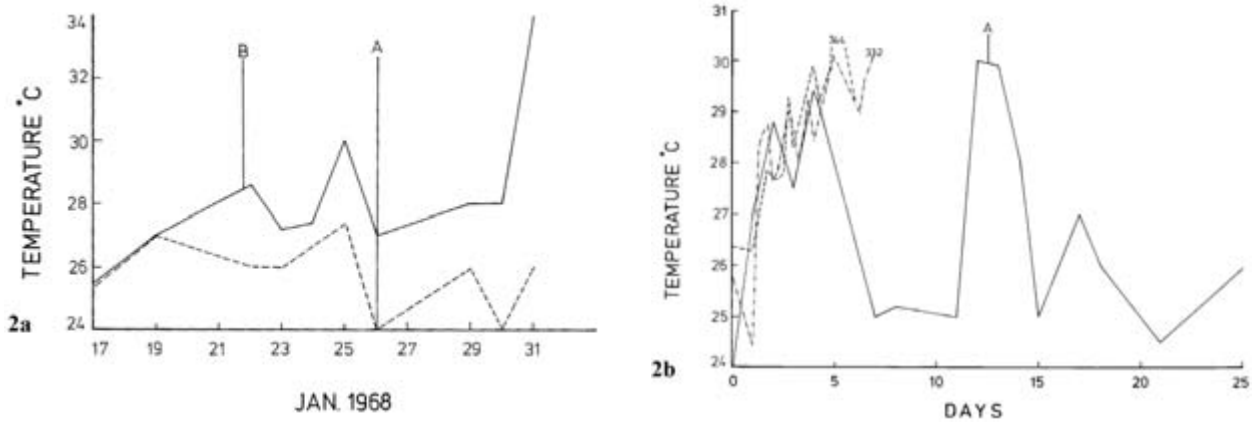


Figure 2a. Daytime pond temperature during first successful breeding in January 1968. (——— surface; - - - - - - bottom). Water was flowing through pond until it was stopped at "A"; B, estimated time of spawning. **2b**. Aquarium temperatures during attempts to induce spawning by raising temperature using aquarium heaters. - - - - - 15 to 21 February 1968 and – • – • – • 14 to 21 February 1968. In both these cases fish were not fed well beforehand and no breeding occurred. ——— 10 March to 4 April 1969. A, fish bred on 21 March 1969 after feeding twice daily for three weeks.

Aquarium trials

On 2 November 1966, 24 fish (50 – 75mm in length) were placed in an aquarium. Within four weeks seven had died, possibly as a result of lack of suitable food and overcrowding. Over the period the pH had risen to 8.2 and the temperature rose from 12.0°C to 24.2°C. No breeding occurred.

Pre-spawning displays were first observed among three adults placed in an aquarium in August 1967, but no breeding occurred. The first breeding in aquaria occurred in February 1968, when water temperatures reached 29.0°C, after 7 adults had been fed well for 3 weeks. Sexes could be readily distinguished as spawning approached. A sudden drop in ambient temperature interrupted this breeding, so heaters were used in the next trials in order to maintain steady temperatures. A further spawning occurred in early 1969, in a heated aquarium at 29.9°C (See Fig. 2b), in which fish had been fed twice daily for three weeks.

In an aquarium holding 2 male and 3 female fish, the temperature was raised from 26.3 to 34.4°C over a period of 7 days, and in another containing 5 male and 6 female fish the temperature was raised from, 24.5 to 33.2°C over eight days (Fig. 2b). In both cases no displays or breeding occurred although one brightly coloured male was observed with the tail partly curved around a gravid female. These fish had been transferred into aquaria from ponds or directly from Willow Dam and had not been regularly fed prior to the anticipated breeding period. Their general condition at the time was not good.

Since increasing temperatures alone were not successful in inducing spawning, attempts were made to induce spawning solely by increasing feeding while maintaining temperatures at a lower constant level. In April 1969, after two weeks of intensive feeding (at least twice daily), pre-spawning behaviour was observed, and in the fourth week at water temperatures of 24.5°C, spawning occurred. Further trials had similar results even at temperatures as low as 22.4°C (Table 2).

In September 1969, 11 fish in an aquarium in an air conditioned room were fed considerable numbers of earthworms twice daily. Breeding commenced 3 weeks later and the fish spawned 12 times on 9 separate days between 12 October and 6 November 1969. Spawning occurred during daylight hours (i.e. 0800 - 1730 hrs) when water temperatures varied from 19.2 to 25.6°C. One of the large female fish received numerous injuries caused by harassment from the male during this spawning period and died shortly after spawning. During 1970 and 1971 six further spawnings were induced by increasing the abundance of food, when temperatures varied between 21.3 and 24.7°C. The adults of the 1971 spawnings were 3 years old, being the progeny of the December 1968 spawning. pH in aquaria during these trials varied from 7.1 to 7.8.

It was concluded that the abundance of food was the most important factor in inducing spawning which could occur over a wide range of temperatures. Sudden drops in temperature could interrupt spawning.

Breeding period in wild populations

In aquaria, spawning was only recorded at temperatures above 19.2°C when an abundance of food was available. In the wild, abundant food would occur only in late spring and summer months or during a flood. Sampling in the Willow Dam area (Fig. 3) indicated an increase in numbers of fish during November the pre-spawning period. The area sampled consisted of a number of channels draining into Barren Box Swamp, a cumbungi swamp (*Typha* sp.), varying between 2673 and 3362ha in area. It seems that the fish move out of the swamp into the channels during this period as the breeding season approaches. Most of the channels where they are found have a thick growth of ribbon weed *Vallisneria gigantea*, which would provide better cover both for fish during spawning and for larvae, than would be present in the swamp itself.

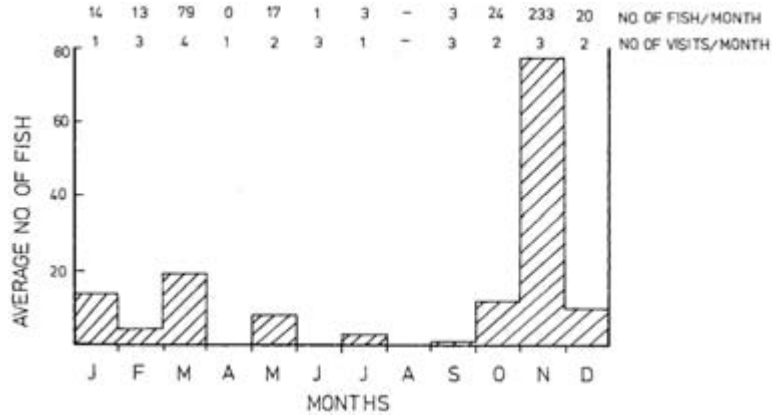


Figure 3. Average number of fish per visit per month caught at Willow Dam. Numbers of fish caught per month and numbers of visits per month also shown. On every visit, sampling was attempted, though only on some occasions were *M. adspersa* caught. Total number of visits 25. Total number of fish caught 407.

Pre-spawning Behaviour

The breeding displays of *M. adspersa* are quite elaborate. As the breeding period approached the blue and purple spots along the sides of the body brightened and the facial stripes became very prominent. Breeding displays were observed in aquaria possessing at least 5 fish. Outside the breeding season these fish lived harmoniously together and did not appear to establish territories, but as the breeding season approached, the males became territorial and loose pairing followed. Territories were normally less than 0.025 m^3 encompassing at least one corner of the tank.

Charging activity, more frequently displayed by the male (Williams 1972) in defence of its territory, was common at this time. As the strength of the pair bond increased, the female commenced to clean a smooth flat object, in most instances the glass sides of the aquarium. On one occasion they cleaned and deposited eggs on microscope slides, a number of which had been put in the aquaria for this purpose. Site cleaning involved excavating but not actually carrying sand, chafing and fin-digging activity as outlined by Williams (1972). Generally the ventral surface of the fish in the region of the pectoral fins contacted the site, while the fins were moved back and

forth alternately in a brush like action. This activity was similar to that used during aeration of the eggs. Charging and site cleaning were often carried out by a pair alternately, and occasionally by unpaired individuals. On one occasion the female tolerated 3 males who charged each other and disputed the territory. This activity faded each evening, but continued during daylight for a week or more. Up to four pairs in a 90L aquaria were seen displaying in this way simultaneously.

As spawning approached, a mutual display, involving gyrating spirals, often occurred some distance from the nest. The pair faced each other at angles of 90° – 120°, pointing upwards with their fins extended, then both rolled over onto their right hand sides, and the female swam alongside the male facing him ventrally, followed by a rapid flick of their tails resulting in a spiral around the longitudinal axis between the fish, their movements increasing in speed until, after approximately one revolution around the axis, they darted off in opposite directions. This was often accompanied by a wriggling motion just prior to the spiral movement. They occasionally rested head up and inclined to one side. If violently disturbed they normally took a couple of hours to settle down again. In aquaria where there were uneven numbers of males and females, some males took up a territory and defended it even though no females were available. On occasions the unpaired male would approach a pair displaying, the paired male would then charge and nip, but the pair never seemed to split up. Periodically the displaying pair would disperse in the aquaria, but after a short period they would return to the territory and resume displaying. When the male was not displaying, he jealously guarded the nesting area and rapidly returned to the selected site at regular intervals to defend it. The intensity of alertness and antagonism to intruders increased as the spawning time approached. Shortly before spawning, both the male and female occasionally nipped or nudged each other in the vicinity of the urino-genital papilla, as if testing the readiness of each other for spawning.

Number and rate of deposition of ova

In the spawning watched in detail on 21 March 1969 (Table 2), 774 ova were laid in 1½ h. The number of ova laid at each attempt after which fertilisation took place by the male is shown in Fig. 4a. The number at each attempt varied from 1 to 31 with a mean number of 11.4, the longest pause in laying being 5 minutes.

The rate of ova laying (ova laid per 10 minutes) reached a peak approximately half way through spawning (Fig. 4b). At times ova were laid at a rate of 1 per second, but over the whole laying period, the rate fell to an average of 1 per 7 seconds.

Spawning behaviour (Fig. 5, 6)

During the early stages of ova laying the female would often approach the male and carry out the spiralling activity. The male would fertilise the ova after each short period of ova laying, but occasionally she would chase him away because she had not finished. During

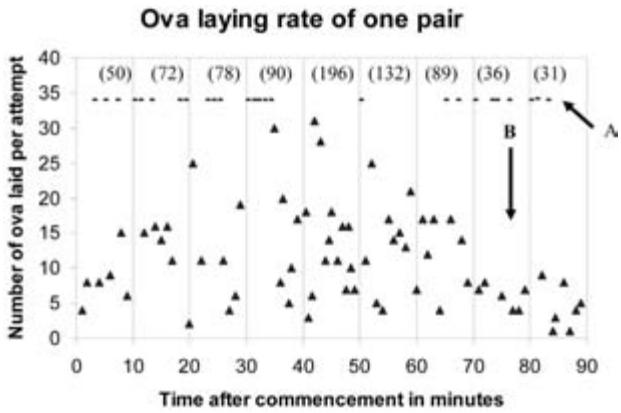
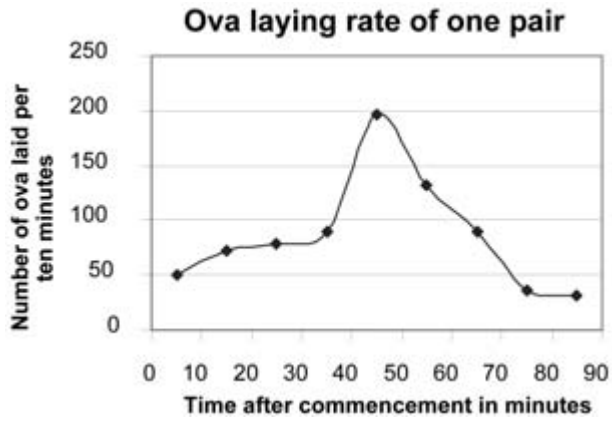


Figure 4a. Ova laying rate of one pair, recorded as numbers of ova laid per attempt. ▲ number of ova laid at each attempt between each fertilisation by the male. Numbers in brackets are numbers of ova laid in 10 minute intervals. A, dashes indicate pauses in egg laying; B. male ate four eggs.



4b. Ova laying rate of one pair in numbers of ova laid per ten minute interval.

egg laying the male stood guard (Fig. 5c) and promptly chased intruders away. During laying the female fanned or agitated the eggs continually with her pectoral fins, while carefully attaching the eggs to the substrate including occasionally, to already attached eggs, by means of a placement type action of the urino-genital papilla and body movement. The urino-genital papillae of the male (Fig. 6c) and female (Fig. 6d) were elongated and swollen. In the female, the papilla extended to approximately 2/3rds the length of the spine of the ventral fin. A dense cluster of eggs covering up to 30 cm^2 in area was formed. Often the female would hunt the male towards the eggs by nudging his abdomen, this activity became more regular as spawning progressed.

Fertilisation by the male consisted of one run usually upwards and downwards across the egg cluster, while waving the urino-genital papilla and leaving a very fine white zig-zag trail of sperm which dissipated after about 10 seconds (Fig. 6e). The time taken for each fertilisation attempt was approximately 6 seconds. One male ate only a few eggs towards the end of spawning, unlike some males which ate large numbers of eggs. As spawning concluded, the female became very vicious towards intruders, until the male chased her off, took charge

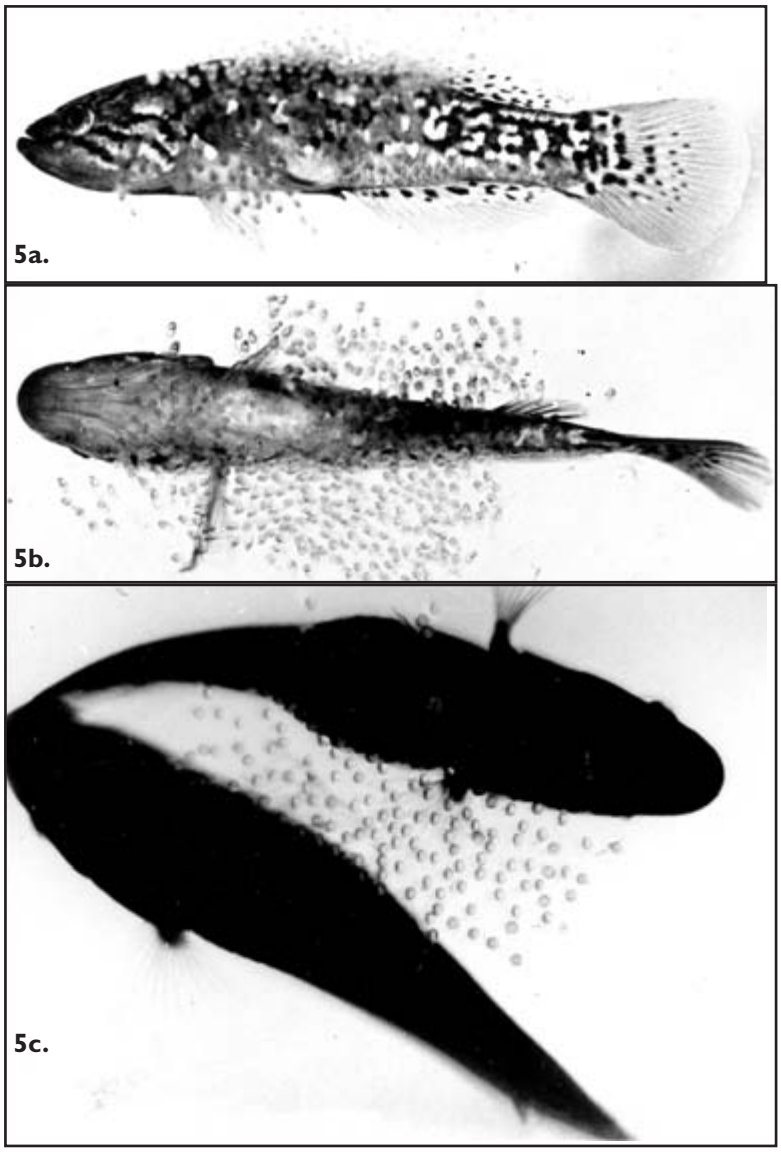
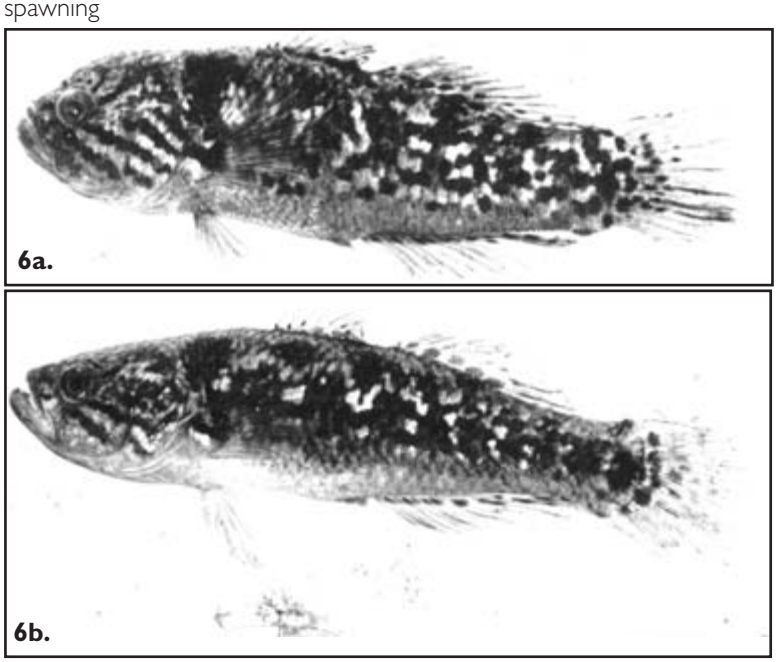


Figure 5. (a) Adult male 10 hours after spawning guarding eggs. (b) Adult male fanning eggs with pectoral fins. (c) Female above, male below during spawning



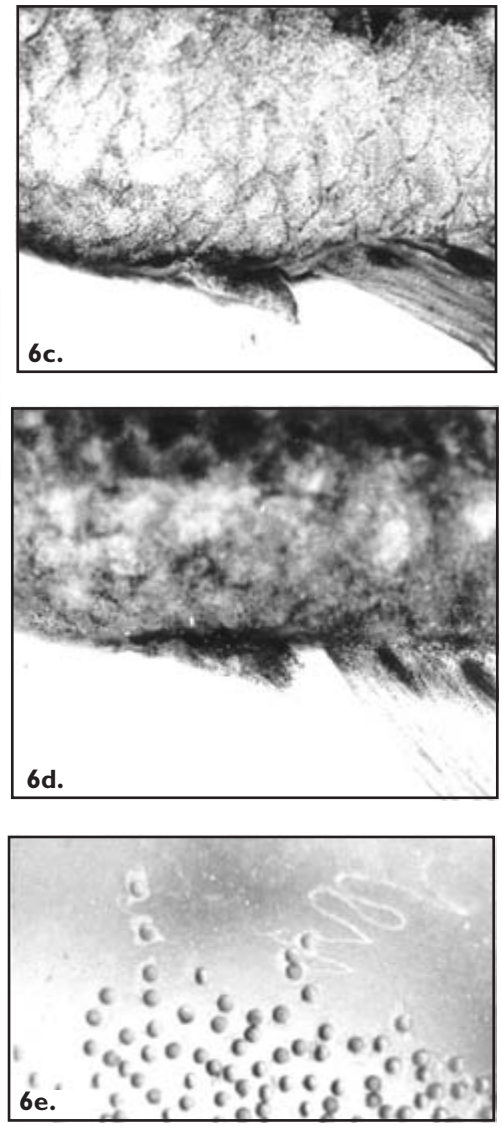


Figure 6. (a) Large adult male *M. adspersa* close to spawning. (b) Adult female *M. adspersa* close to spawning; note tattered tail through fighting. (c) Close up of urino-genital papilla of male during breeding season. (d) Close up of urino-genital papilla of female during breeding season. (e) Eggs of *M. adspersa* during spawning showing dissipating sperm trail. (f) Base of egg showing threads of adhesive disc and pitted nature of shell.

(Fig. 5a), and commenced fanning and agitating the eggs (Fig. 5b). The pelvic girdle was brought into close proximity with the eggs (Fig. 5b) using the pelvic fins as motionless struts, while the pectoral fins were beaten in an alternate fashion brushing the eggs, sometimes quite violently. Agitation, involving rapid or slow fin-beating, was carried out at 10 to 30 second intervals for half the time during day light hours only. During darkness the male rested alongside the egg cluster. When adult fish were removed from the aquarium after egg laying the incubation period was longer, a higher percentage of eggs died possibly through siltation, and many hatching larvae experienced difficulty in escaping from the egg shell. The agitation process often knocked the top off or split the side of the egg, or knocked the hatching larvae out of the egg. It was concluded that agitation aided in aeration, de-siltation and hatching. On occasions, adults would feed on hatching larvae. This was minimised by placing a clump of fine aquatic plants such as *Chara* sp. below the egg cluster, into which the larvae fell and found some protection. The adult male remained brightly coloured and extremely antagonistic towards other fish until hatching was complete, at which time the site was vacated.

Embryonic Development of eggs

The eggs of *M. adspersa* (Fig. 7) were transparent, elliptical, demersal and possessed an adhesive disc at one of the narrow (generally blunter) ends comprised of adhesive strands (Fig. 6f) which appeared to have hundreds of little hooks. The remainder of the chorion is non-adhesive and appeared pitted using phase contrast microscopy (Fig. 6f). On the inside of the chorion were lines of cytoplasm, criss-crossing and running diagonally around the egg. A few small hairs with a broader basal region were attached to the chorion externally. At spawning pre-morphogenetic organisation of the ovum was still occurring (Devillers 1961), cytoplasm slowly moving towards the blastodisc during bipolar differentiation, carrying with it numerous oil globules which were dispersed throughout or around the yolk (Fig. 8c and d). The egg during this phase changed from a centrolecithal to a heavily telolecithal type (Manner 1964), which ultimately gave rise to meroblastic or discoidal cleavage. At spawning no perivitelline space

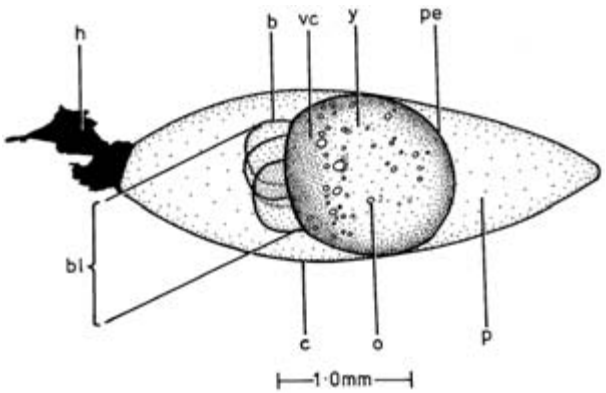


Figure 7. Egg of *M. adspersa* 2h 5min after fertilisation (four cell stage). b, blastomere; b1, blastodisc; c, chorion; h, adhesive disc; o, oil globule; p, perivitelline space; pe, extraembryonic periblast; y, yolk; vc, vitelline syncytium.

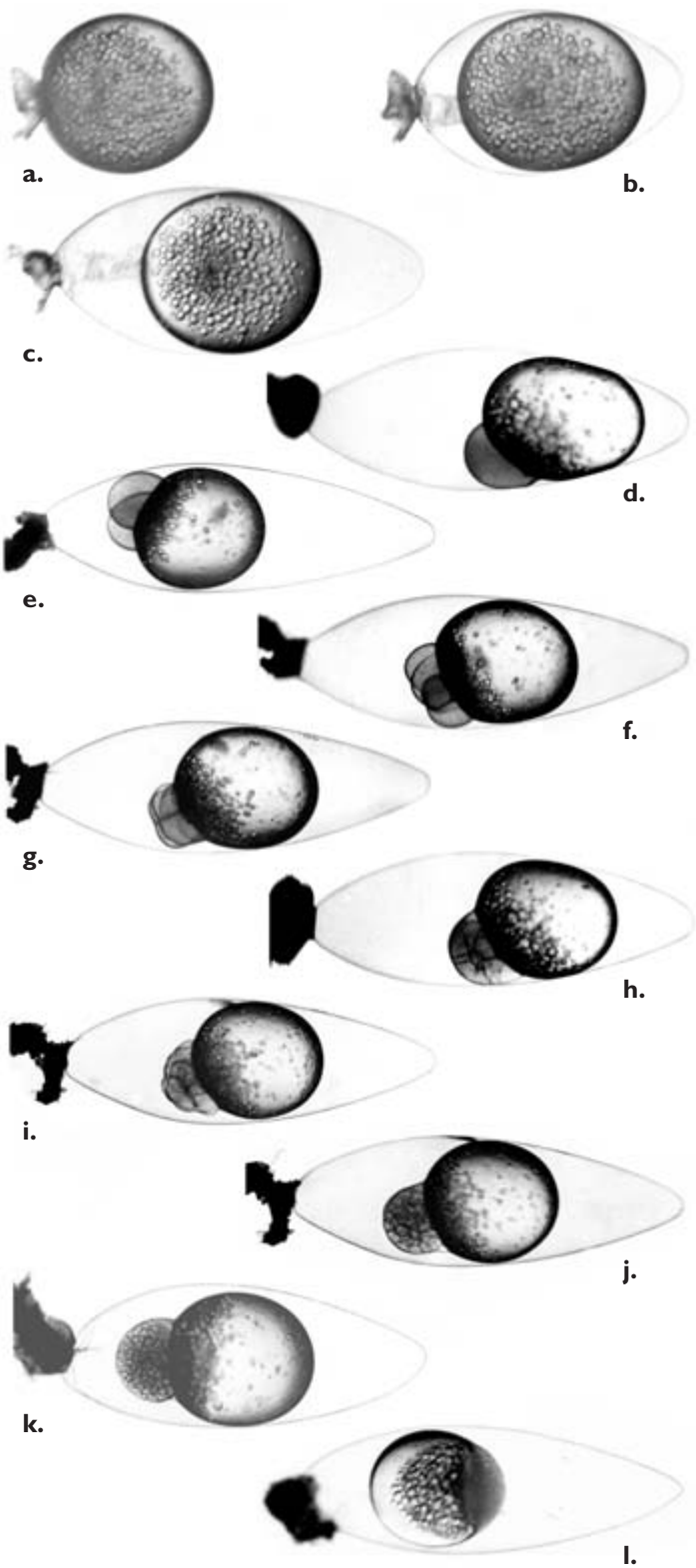


Figure 8. Eggs of *M. adspersa*. Times given are after fertilisation in hours (h) and minutes (min). (a) 0min - before chorion starts to enlarge; (b) 9min - chorion not fully enlarged; (c) 17min - chorion fully enlarged; (d) 1h 17min - 1 cell stage; (e) 1h 40min - 2 cell stage; (f) 2h 5min - 4 cell stage; (g) 2h 30min - 8 cell stage; (h) 3h 10 min - 16 cell stage; (i) 3h 45min - approximately 32 cell stage; (j) 4h 10min - early blastoderm forming a knob of cells; (k) 5h 30min - early blastoderm, individual cells still visible; (l) 8h 10min - blastoderm, cells no longer visible.

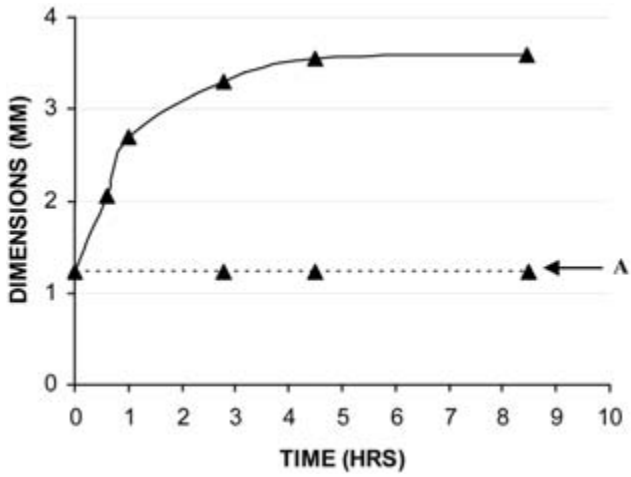


Figure 9. Distension or swelling of chorion during water hardening immediately after spawning plotted against time. ▬▬ length of egg; ------ width of egg. A, no change in width.

existed (Fig. 8a), but on contact with water and after fertilisation, distension and then hardening of the chorion (shell), the perivitelline space formed (Fig. 8a-d). The egg distended along the axis passing through the basal disc (length plot in Fig. 9). The axis at right angles to this (width plot in Fig. 9) showed little or no distension. Water temperatures during development varied between 20.2 and 29.0ºC (Figs. 8, 10 and 11). Normal development occurred within this range, although its rate increased, and egg mortalities were highest at high temperatures, as has been shown also by Piavis 1961), Lagler *et al.* (1967) and Edsal (1970) for other fish species.

Newly spawned nearly spherical eggs varied in diameter from 1.07 to 1.33mm (Mn ± sd 1.17±0.05, n = 58). The length increased to 2.03 to 3.78mm (Mn ± sd 3.06±0.43, n = 58) when water hardening had ceased. Prior to chorion distension, the yolk size equalled the egg size, since no perivitelline space was present. After distension had occurred the yolk was generally slightly flattened; its diameter running through the animal and vegetal pole varied from 0.63 to 1.19mm (Mn ± sd 0.98±0.10, n=42) while at right angles to this it varied from 0.89 to 1.33mm (Mn ± sd 1.06±0.08, n=42).

The hundreds of small randomly distributed oil globules (0.02 - 0.13mm in diameter) at spawning (Fig. 8a) had accumulated at the animal pole by the commencement of cell division or soon after, but still remained very small (Fig. 8d 1h 17min after fertilisation). Normally the yolk was wedged centrally within the elliptically shaped chorion leaving a large perivitelline space between the chorion and yolk, at both pointed ends, but sometimes it was lodged towards one end (Fig. 8d). The chorion was approximately 0.01mm thick. Based on close observations of a single egg at temperatures between 22.2 and 24.7ºC, the fully distended first cell (0.73mm in diameter) underwent its first cleavage at 1h 20min. However, in eggs at lower temperatures, the first cleavage occurred at 2h. The time between cleavages for the two celled (Fig. 8e), four-celled (Fig. 8f) and eight celled (Fig. 8g) stages were 35min, 30min and 30min respectively and the sizes of the blastomeres were 0.54, 0.45 and 0.30mm respectively. From this point onwards in development, it was not possible to follow the periodicity of cleavage, but only its general pattern.

The knob of cells (blastoderm) estimated as 16 and 32 cell stage in Fig. 8h and 8i (0.75mm across) continued to grow (Fig. 8j and 8k, 0.82mm across). Eight hours after fertilisation the individual cells were no longer visible and the blastoderm started to flatten (Fig. 8l) as it commenced to spread over the yolk at the commencement of epiboly (Fig. 10a, 11h 25min after fertilisation). The small oil globules dispersed throughout the yolk again as epiboly progressed and the blastoderm reached almost halfway around the yolk (Fig. 10b, 14h 40min). The thickening of the germ ring forming the embryonic shield (now 0.88mm in length) was clearly visible when the yolk was 2/3rd covered by blastoderm (Fig. 10c). Soon the neural tube area thickened, accompanied by the commencement of neuralation (Fig. 10d). The neural groove was 0.06mm and the neural ridge 0.91mm in width. Epiboly continued, eventually forming a yolk plug at 20h when the yolk was ¾ covered by blastoderm and the embryo showed little differentiation but was 0.93mm in length (Fig. 10e). Dispersion of the oil globules throughout the yolk was still not quite complete. Blastopore closure occurred at about 22h after fertilisation when gastrulation terminated.

Differentiation of tissues into various embryonic structures started at 23h (Fig. 10f) when the cephalic region enlarged and the optic vesicles (0.19 x 0.26mm) appeared. When the embryo, was curled half way around the yolk (Fig. 10g) (length1.51mm, head width 0.29mm) and approached half the length of the egg (Fig. 10h. 1d 5h), the subcaudal and subcephalic folds, separating the tail and the head of the embryo from the yolk, appeared. Somitic divisions, marking the myotomes in the caudal region, soon appeared (Fig. 10i), when the first tail movements were observed. Enlargement of the pericardial sinus commenced at 1d 12h 47min (Fig. 10j), when the eye lens (0.10mm) and the ventral fin fold appeared and the embryo (2.71mm) approached ¾ the length of the egg. In eggs still attached to a substratum, the embryos orientated themselves above the yolk. Most embryos wriggled or twitched in as little as two second intervals. Melanophores appeared along the tail, around the yolk and a few on the head at 1d 19h 20min (Fig. 10k, embryo length 2.96mm). Soon the heart was observed beating (52 bpm.). At 2d 7h 30min both the dorsal and ventral fin folds increased in area and the otic capsules (0.11 x 0.07mm) appeared (Fig. 11a). In some, melanophores formed a continuous line along the dorsal edge of the musculature of the tail and were also numerous along the ventral edge. The eyes now started to darken, their edges darkening first (Fig. 11c-f). A few very early hatchings commenced at this stage (3d 3h), when blood pigmented pale red was first observed passing along the tail. The embryo readily re-orientated itself within the egg by body flexing (see Fig. 11b and c). The embryo (3.89mm) now exceeded the length of the egg (Fig. 11d), while the pericardial sinus continued to enlarge and the buccal cavity first appeared. The eye pigment darkened progressively (Fig. 11f), becoming fully pigmented at about 3d 11h (Fig. 11g (eye diameters 0.36 by 0.29mm, pupil

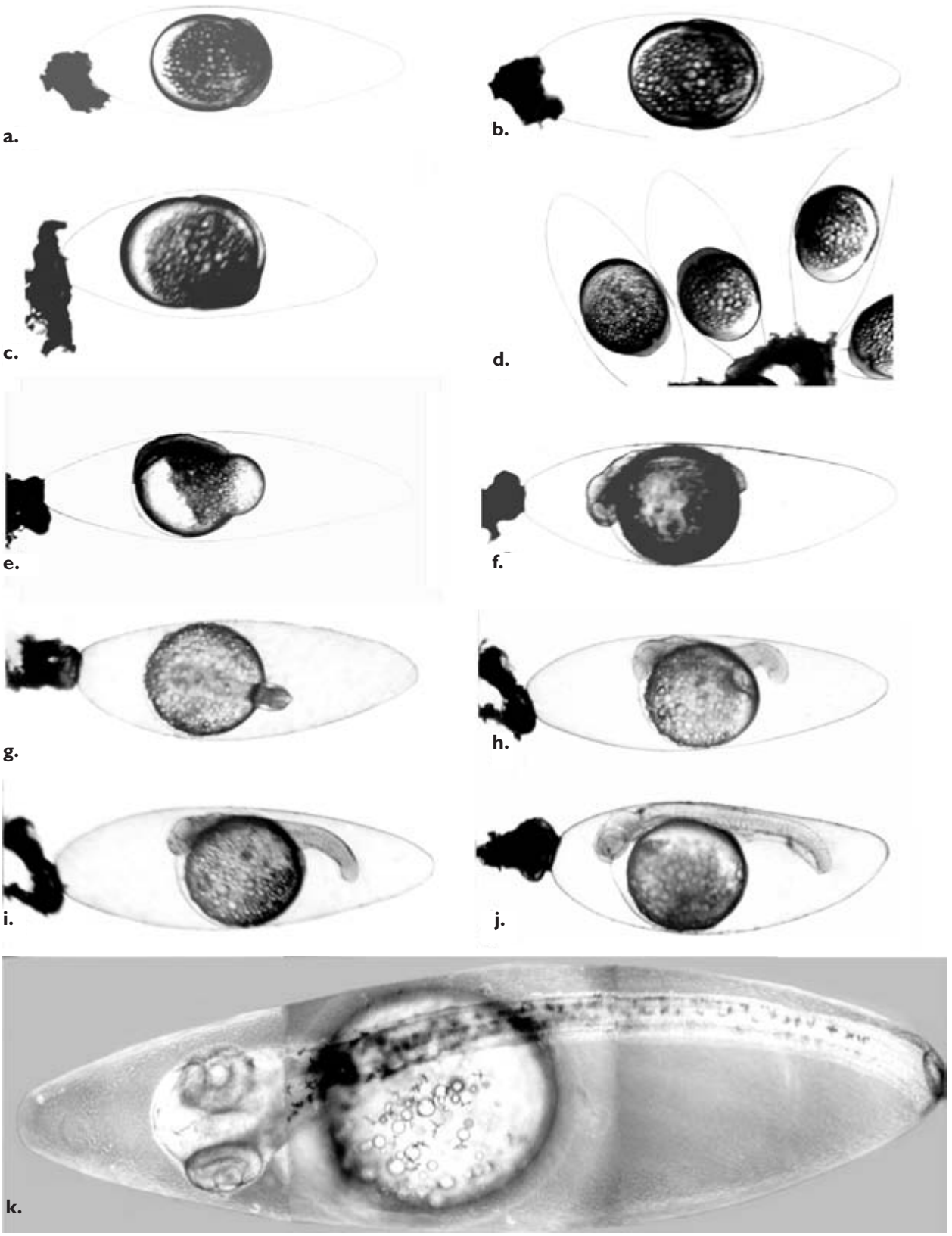


Figure 10. Eggs of *M. adspersa*. Times given are after fertilisation in days (d), hours (h) and minutes (min). (a) 11h 25min - epiboly just commencing; (b) 14h 40min - epiboly showing germ ring; (c) 14h 40min - epiboly with embryonic shield; (d) 14h 40min - group of eggs at same stage of development showing commencement of neuralation; (e) 20h - yolk plug and early embryo; (f) 23h 20min - enlargement of cephalic region and early development of optic lobes; (g) 1d 3h 36min - ventral view of early development stage of head and optic lobes; (h) 1d 5h 2 min - tail first free from yolk; (i) 1d 12h 16min - somitic divisions of tail apparent; (j) 1d 12h 47min - early stages of development of somitic divisions, eye lens and fin folds; (k) 1d 19h 20min - phase contrast showing first signs of melanophores and chromatophores on yolk and tail.

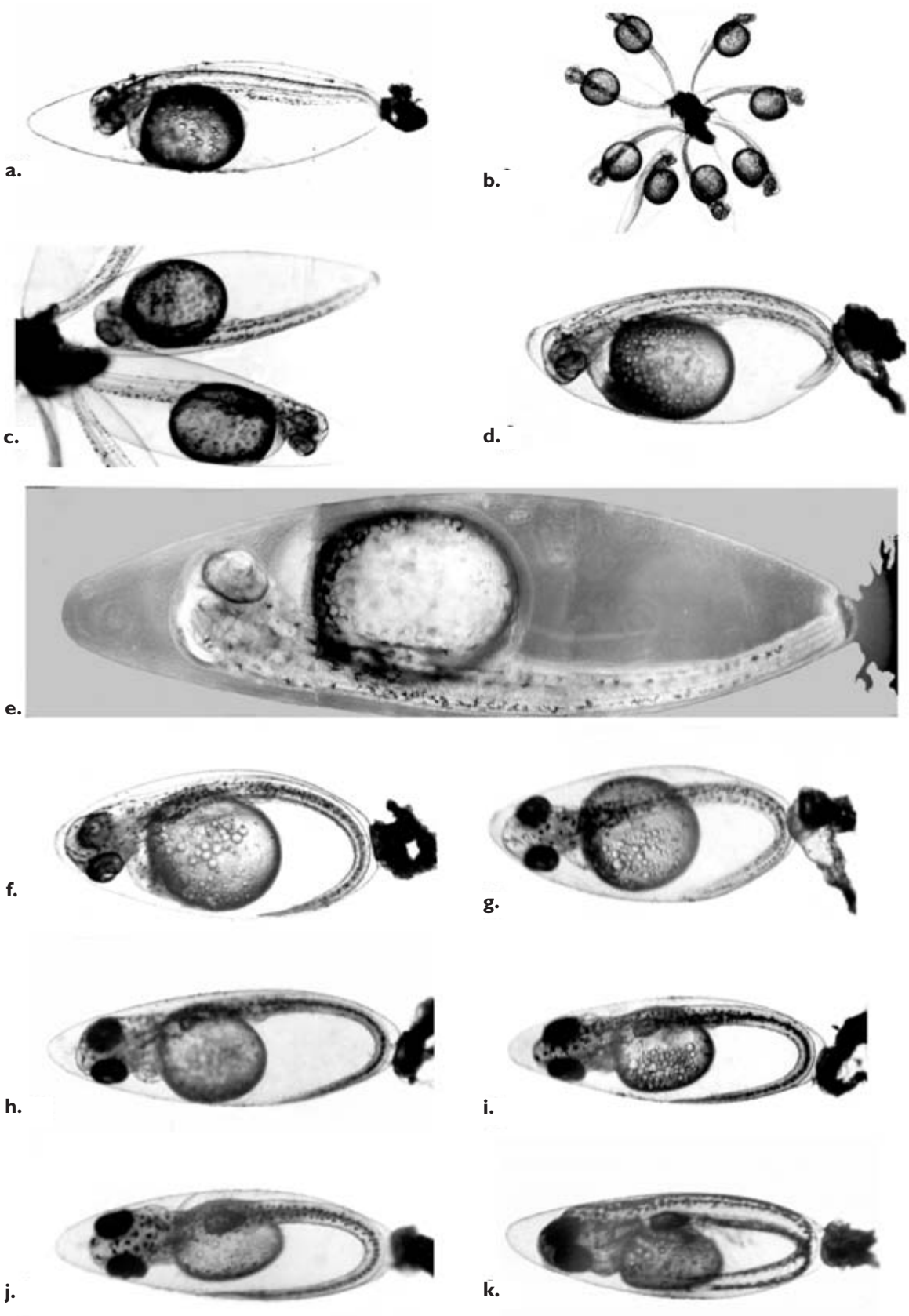


Figure 11. Eggs of *M. adspersa*. Times given are after fertilisation in days (d), hours (h) and minutes (min). (a) 2d 7h 30 min - fin fold increasing in area; (b) 2d 8h - cluster of eggs as laid; (c) 2d 10h 55min. cluster of eggs with eyes just starting to darken and showing varying embryo orientation; (d) 2d 13h 30min - larvae more than full length of egg and showing heart; (e) 2d 12h - phase contrast showing distribution of pigment cells and the optic capsules; (f) 3d 3h 4min - eye pigment darkening; (g) 3d 11h 23min - eyes fully pigmented; (h) 4d 4h 9min - swim bladder first appears; (i) 4d 22h 4min - first signs of diminishing yolk; (j) 5d 11h - pectoral fins; (k) 5d 18h 3min - swim bladder well developed.

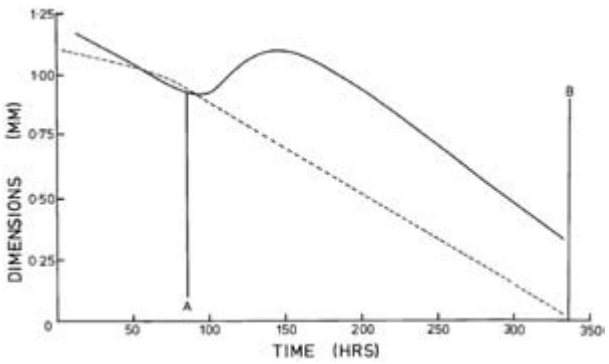


Figure 12. Relationship between length of yolk (——) and width of yolk (- - - -) and hours after fertilisation, indicating reshaping after hatching. A, time at hatching; B, commencement of exogenous feeding (i.e. yolk completely utilised).

diameter 0.10mm, head width 0.86mm)), and the embryo was coiled ¾ of the way around the circumference of the egg. The swim bladder appeared at 4d 4h 9min (Fig. 11h), rather small at first but soon attaining a size of 0.36 x 0.24mm (Fig. 11i). Melanophores continued to increase in number and size. The line of pigment along the dorsal edge of the tail and the numerous large melanophores on the top of the head and on the body above the yolk (Fig. 11i and 11j) were now prominent. At 5d 11h the pectoral fins (0.31mm in length) were quite noticeable (Fig. 11j). During this stage the yolk sac increased in length (Fig. 11k and 12) streamlining the shape of the embryo, and the yolk volume did not appear to diminish so rapidly, possibly due to the development of the gut in this region. When yolk sac reshaping was complete, the rate of use of yolk increased again.

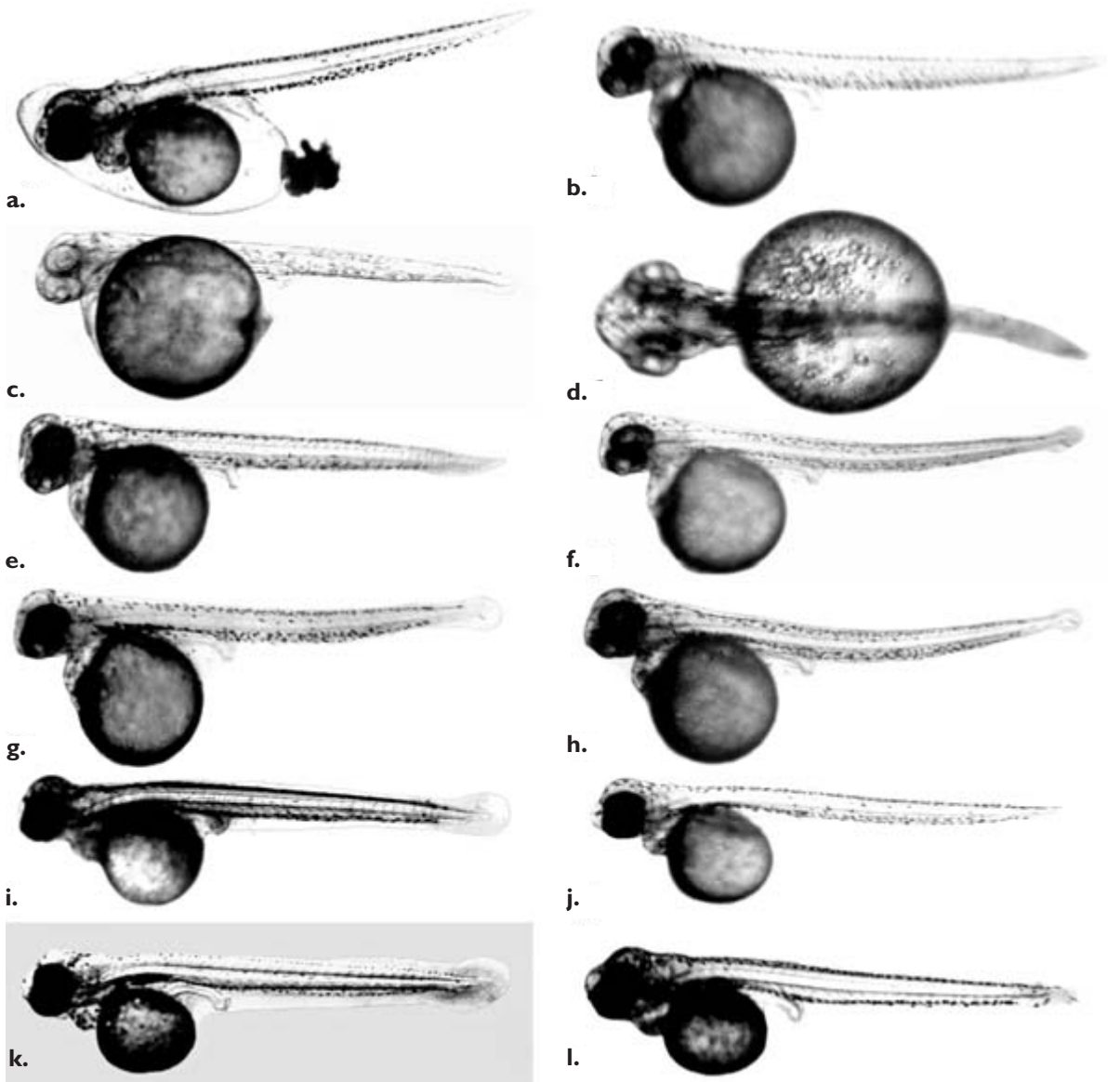


Figure 13. Larvae of *M. adspersa*. Times given are after hatching in days (d), hours (h) and minutes (min). (a) 5d 18h 20min after fertilisation - larva hatching tail first, with a distinct dorsal and ventral band of melanophores. (b) - (j) shows a series of larvae which hatched at varying stages of development. (b) 0min - lateral view; (c) 0min - lateral view, early hatched larvae with unpigmented eyes; (d) 5min - dorsal view; (e) 30min lateral view showing developing melanophores; (f) 31min - lateral view of larvae at an earlier stage of development than Fig. 13 (e); (g) 3h 16min - lateral view of same larvae as Fig. 13 (f); (h) 7h 2 min - lateral view of same larvae as Fig. 13 (f); (i) 12h - lateral view showing fin fold; (j) 19h 6 min - lateral view of same larvae as Fig. 13 (f); (k) 1d 8h 50min - lateral view of same larvae as Fig. 13 (f); (1) 1d 17h 55min - myotomes of tail.

As hatching approached the movements of the embryo increased in intensity, causing the whole chorion to flex and distort, become flaccid and lose its turgidity. Eventually the chorion split or the end of the egg broke off, and usually the tail of the larvae emerged first (Fig. 13a). The prolarvae, as they are now known, continued to thrash with their tail in an effort to free the head from the chorion. Prolarvae of eggs removed from the rather violent fanning movements of the adult male, often experienced difficulty in freeing themselves from the chorion, which shrivelled up around their yolk and head and could cause them to die. Fanning of the eggs by adults while the eggs were still attached by their basal attachment seemed to assist hatching and probably shortened the hatching time. In one batch of eggs attended continuously by the adult, hatching started at 3d 3h after fertilisation and took a further 3d 20h to complete hatching. Even though eggs were laid over a short period of 1½-2h, a high variation in time to hatching occurred, depending on the temperature (see also Needham (1942) and Konstantinov (1957) for other species). Most larvae, however, hatched at about 4d after fertilisation. The longest hatching period recorded was 8d 8h which were for eggs retained in petri dishes.

The heart rate of embryos, first observed beating at 1d 21h at 52 bpm seemed to increase with age. The heart rate was 110bpm at 2d 2h, and 175bpm. (range 140 - 204 bpm., n=15) at 4d 10h when they hatched. Movement of the embryo was first observed at 2d 8h.

Prolarva

The terminology used in the subdivision of larval stages is based on Hubbs (1943), the prolarva being the term used when the larva still possesses yolk.

The yolk, initially spherical, diminished in volume and reshaped during egg and prolarval development (Fig. 12). Toetz (1966) measured this by determining yolk volume. The exact point indicating the termination of the prolarval stage (i.e. the yolk size approaching zero in Fig.12) is often difficult to determine because it is masked by the developing gut and the presence of food in the gut.

Water temperatures during prolarval and early post-larval development varied between 20.3 and 29.0^{O}C in petri dishes and 19.0 to 22.8^{O}C in aquaria. At hatching the prolarvae varied from 3.44 to 4.15mm in length, and the yolk in early hatched prolarva measured approximately 0.95mm in diameter. The general structure of a prolarva is shown in Figure 14.

Because of the different ages of larvae at hatching, the developmental stage varied considerably. For example the variation in eye and body pigmentation close to hatching can be seen in Figs 13a-j. Salient features appearing in prolarvae near hatching were the small pectoral fins, the myotomes of the tail and the simple sucker like mouth, all directly associated with the change in environment the larva experienced at hatching.

Melanophores were concentrated into bands of pigment along both the dorsal and ventral edges of the musculature of the prolarva, extending anteriorly over the head dorsally and to the yolk ventrally. Approximately 20 prominent melanophores usually developed on the pericardial wall. All prolarvae discussed from here on (Fig, 13k onwards) hatched at approximately the same stage of development, 4d after fertilisation.

After hatching the oil globules were dispersed throughout the yolk, and the pupil of the eye was dark olive in colour. The fin fold surrounding the caudal region commenced dorsally 2/3 of the way along the yolk. For dimensions of structures at the time of hatching (egg / prolarva) see footnote[1]

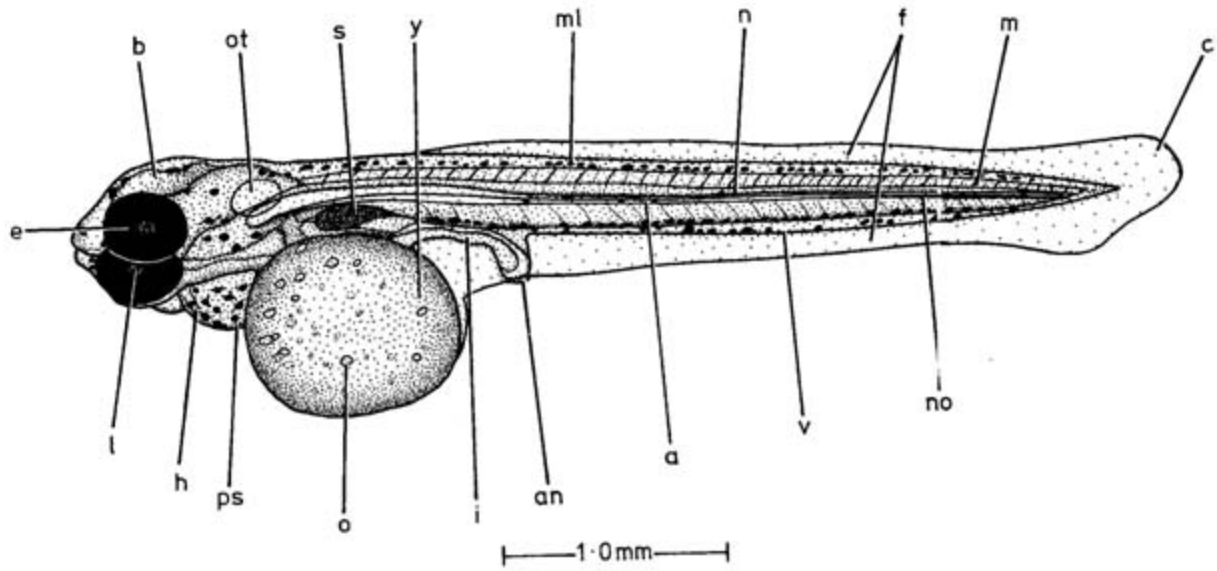


Figure 14. Prolarva 1d 8h 50min after hatching. a, aorta; an, anus; b, brain; c, caudal fin fold; e, eye; f, fin fold; h, heart; i, intestine; l, lens; m, myotomes; ml, melanophores; n, neurochord; no, notochord; o, oil globules; ot, otolith; ps, pericardial sinus; s, swim bladder; v, caudal vein; y, yolk sac.

1 Dimensions at hatching oil globules 0.04 - 0.19mm, heart – length 0.34mm and width 0.23mm, eyes 0.37 x 0.29mm, lens 0.11mm, depth of body at anus 0.51 and at yolk 1.04mm, head width 0.87mm, otic capsules 0.11 x 0.17mm.

In aquaria the larvae sank passively to the bottom as they hatched, but soon became lively and swam by means of rapid tail movements. Only on one occasion were they observed to swim actively and be neutrally buoyant at the time of hatching.

At about 1d 9h after hatching, the swim bladder (0.39 x 0.24mm) started to become opaque and pigmented (Fig. 13k), and the yolk elongated and narrowed (Fig. 12, 13k and 13l). The fin fold expanded in the posterior caudal region and the heart re-orientated from a vertical to a horizontal plain. At 1d 8h 30min after hatching, large stellate melanophores occurred in the cardiac region and branchiostegal rays (Fig. 15a) and the prominent lower jaw with its bone elements (Fig. 15b and 15c) appeared. Abnormalities like the shorter dorsal fin fold (Fig. 15b) and the notch in the caudal fin fold (Fig. 15d) were common. The heavily pigmented melanistic

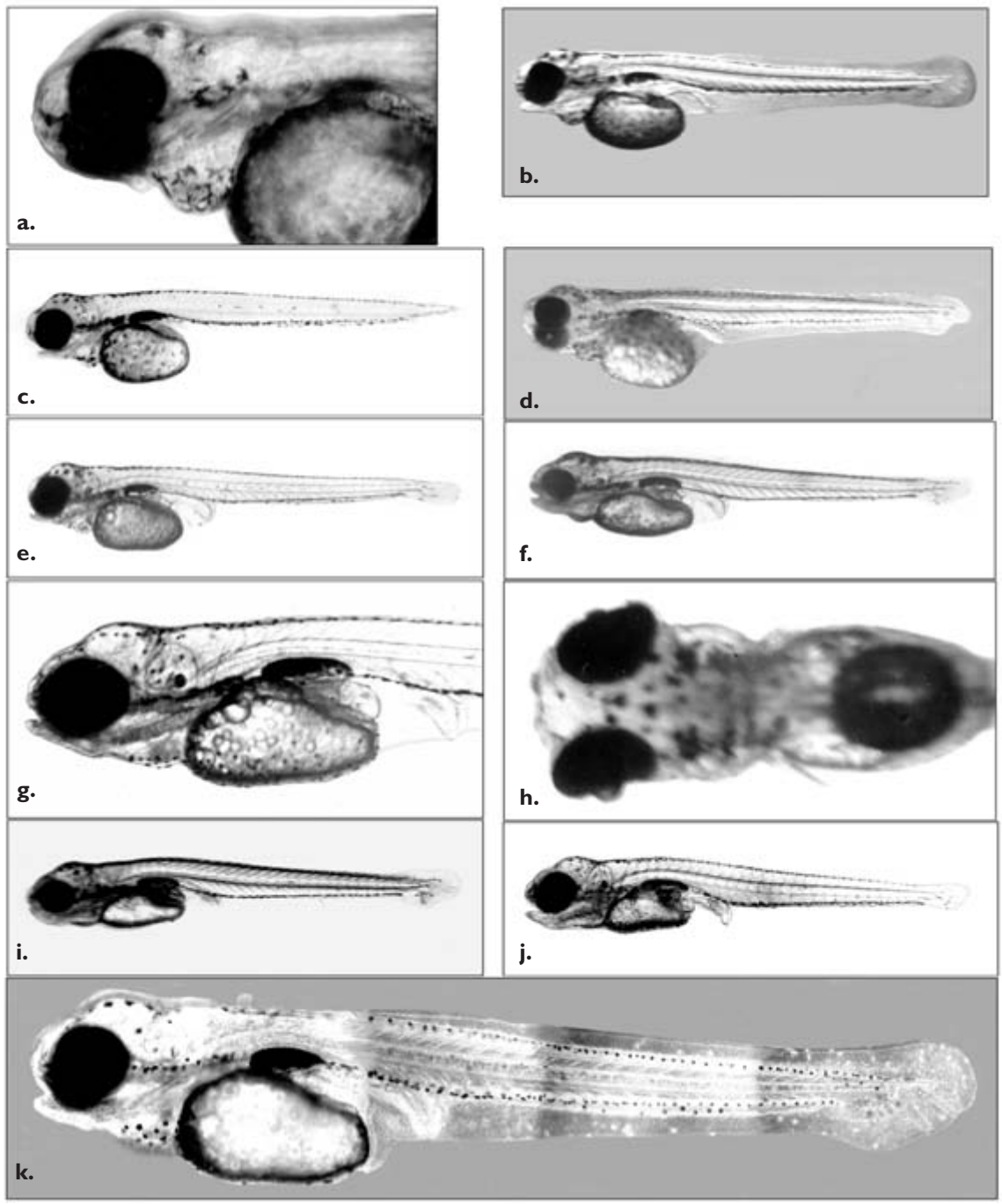


Figure 15. Larvae of *M. adspersa*. Times given are after hatching in days (d), hours (h) and minutes (min). (a) 1d 18h 30min - lateral view of head, branchiostegal rays, and melanophores around cardiac region; (b) 2d 2h 45min - well developed jaw and diminishing yolk; (c) 2d 7h 57min - marked dorsal and ventral pigment band; (d) 2d 7h 58min - abnormal notch in tail and dispersed oil globules in yolk; (e) 2d 9h 8min - pigmented dorsal side to swim bladder; (f) 3d 15min - distinct mytomes, swim bladder elongating and yolk sac diminishing further; (g) 3d 9h 41min - lateral view of head region showing otic capsule and developing intestine; (h) 3d 16h 6min - dorsal view of head region showing eye lenses, pectoral fins and oval swim bladder; (i) 3d 19h 45min - lateral view, upturning of tail and fin rays first appearing; (j) 4d - lateral view; (k) 2d 9h 39min - lateral view, composite photo, phase contrast, showing tail structure and arrangement of melanophores.

dorsal region of the swim bladder darkened, while ventrally it remained silver (Fig. 15e). An organ, probably the liver, appeared ventro-posteriorly to the swim bladder at 2d 10h (Fig. 15e and 15f), and the dorsal fin fold now extended to the mid point of the yolk as it continued to elongate and narrow (Fig. 12 and 15f).

At this stage, prolarvae swam vigorously to the water surface in a spiral movement, and then sank slowly while in a resting state. Their jaws moved quite actively. No further melanophores appeared in prolarvae since hatching (now average length 5.67mm (3d)), so that the distance between melanophores had increased, spreading them into a line both dorsally and ventrally (Fig. 15k). Details of the musculature, vertebrae and neural spines of the caudal region can be seen in Fig. 15k (phase contrast). This also shows the speckled nature of the caudal fin folds, and the alignment of some tissues indicating the commencement of fin ray formation. Opercular movement, indicating the pumping of water through the gill chambers, had now commenced. At 3d 9h 41min (Fig. 15g), a few small to medium sized oil globules appeared at the anterior end of the yolk, the otic capsule measured 0.3mm and the intestine developed rapidly. The eye lens and cornea were protuberant and the swim bladder was heavily pigmented dorsally (Fig. 15h). The prolarvae now swam actively, horizontally for prolonged periods using pectoral fins (length 0.4mm), and although the yolk was not completely used up, a pale yellowish pigment occurred in the gut indicating the commencement of active feeding. Fin rays in the caudal fin and a slight upturning of the notochord of the tail appeared at 3d 19h (Fig. 15i) and the fin fold started to diminish around the caudal peduncle (Fig. 15j and 18a). Melanophores were still prominent along the body, on top of the head posterior to the mid eye region (approx. 40) (Fig. 16a) and ventrally on the yolk (Fig. 18a). The prolarvae

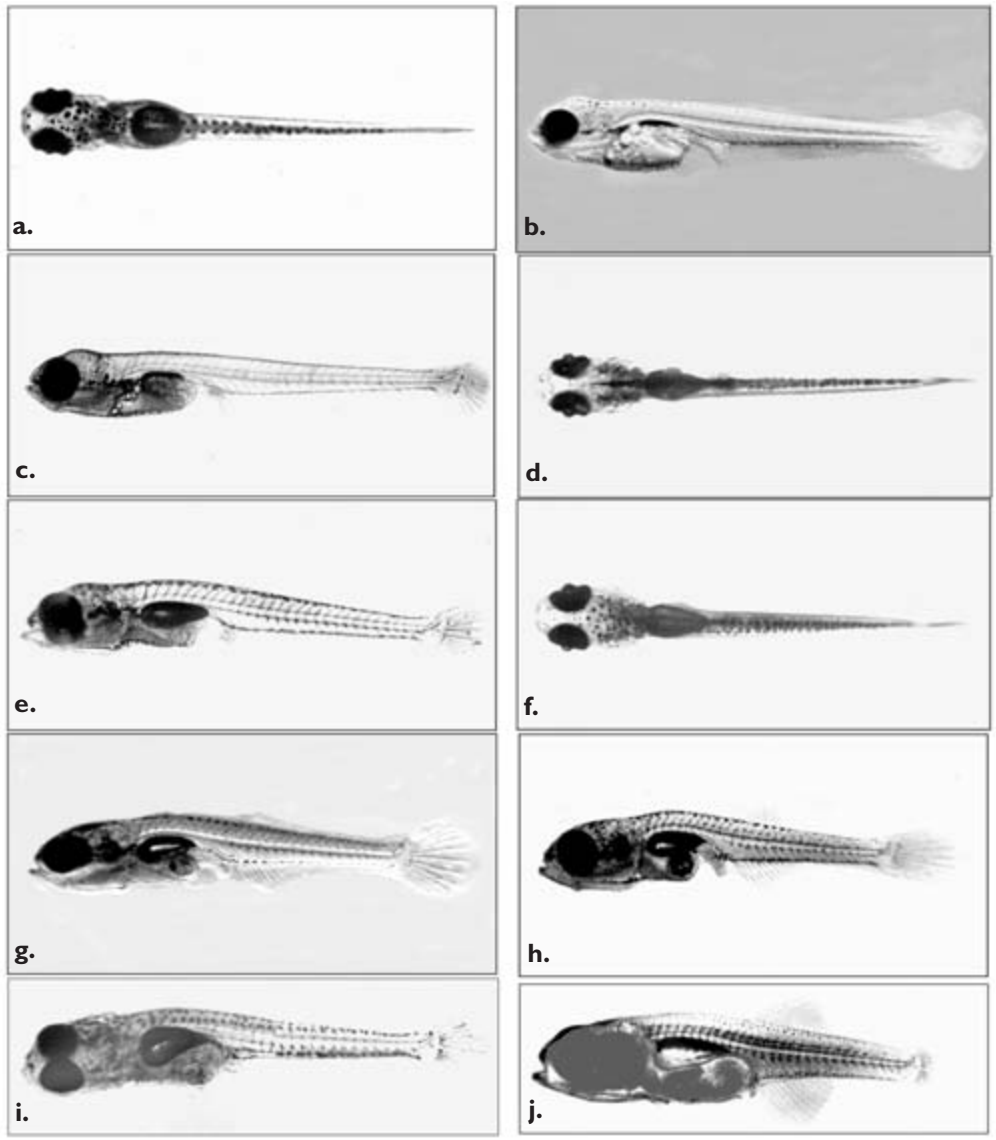
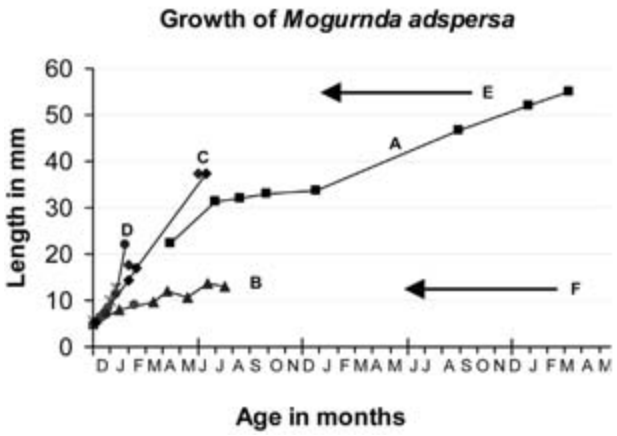


Figure 16. Larvae of *M. adspersa*. Times given are after hatching in days (d), hours (h) and minutes (min). a) 4d - dorsal view, melanophores on dorsal region with single row on each side of tail, and pectoral fins visible; (b) 4d 8h 36min - lateral view showing fin rays on caudal fin; (c) 6d 15h 13min - lateral view, marked upturning of vertebrae in tail, faeces in intestine; (d) 7d - dorsal view, increasing pigment on top of head; (e) 7d - lateral view, showing yolk completely used up; (f) 9d - dorsal view, swim bladder elongating; (g) 12d - fin rays developing in dorsal and anal fins, fin fold nearly gone; (h) 17d - lateral view showing well developed jaw; (i) 17d - dorso-lateral view, upturning of tip of vertebrae, full intestine; (j) 29d - well developed dorsal and ventral fin, swim bladder silvery in colour pigmented dorsally, numerous small melanophores appearing.



were now quite streamlined (Fig. 16b) since the yolk had nearly gone and only a few oil globules remained. Greenish yellow faecal matter was obvious in the intestine at 6d 15h (Fig. 16c) when peristaltic movements were first observed. Yolk was noticeably absent a few hours later (Fig. 16d). As soon as the yolk and oil globules were utilised the larvae became buoyant and were able to float almost motionless at the water surface while feeding; the utilisation of food stores and growth of the swim bladder apparently altering their buoyancy. This marked the conversion from endogenous to exogenous feeding and the completion of prolarval development, which occurred at 6d 15h after hatching. It also marked a critical stage in larval development when high mortalities often occurred (Toetz 1966).

Figure 17 Growth of *M. adspersa* assuming all breeding commences in December. A, kept in aquaria with ample food supply; B, kept in aquaria with minimal food supply: C kept in ponds; D one sample of rapid growth in ponds; E, length at which aquarium reared fish first bred; F, length at which stripes first appear on operculum.

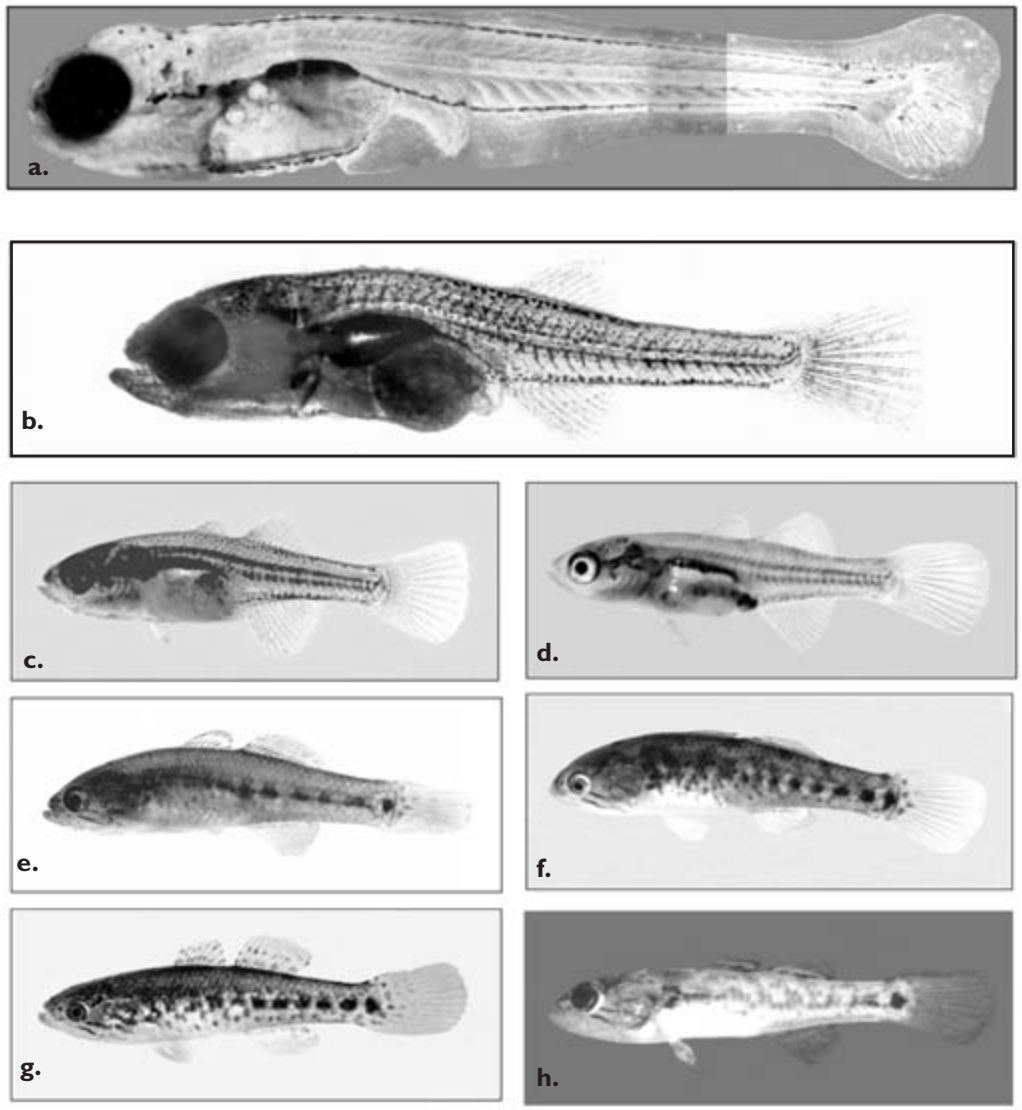


Figure 18. Larval and juvenile *M. adspersa*. Times given are after hatching in days (d) and hours (h). (a) 4d 23h - lateral view, composite photo, phase contrast showing detailed structure; (b) 33d - lateral view, composite photo showing detailed structure and melanophores on the fins; (c) 39d – 11.5mm in length, small pigmented spot behind eye; (d) 41d - anterior dorsal fin well developed, eye with silvery covering, minute melanophores developing; (e) 45d - dermal pigment spots along lateral line and opercular stripes first appeared, completely covered in scales; (f) 55d - dermal pigmentation intensifying; (g) 80d - pigmentation similar to adult fish with pronounced spots on fins; (h) 100d - a paler form.

Post Larvae

Hubbs (1943) defined the post-larval stage as "Larva following the time of absorption of yolk; applied only when the structure and form continues to be strikingly unlike that of the juvenile."

Recently formed post larvae (6d 15h after hatching; 10d 15h after fertilisation) were 5.30 to 5.85mm in length (mean 5.50mm, n=4) (commencement of plot Fig. 17). Other measurements of post larvae are provided in footnote[2]. The heart beat ranged from 200 to 240 bpm at 27.3^{o}C (n=10 one larva), while larva rested. The fin rays were starting to appear in the posterior dorsal fin and were present in the pectoral and caudal fins (Fig. 16e). Approximately 28 large, evenly spaced pigment spots (Fig. 16f) occurred along each side of the mid dorsal line, near to each of the myotomes which were separated by haemal spines. Soon the swim bladder elongated becoming pointed posteriorly and filled most of the dorsal portion of the abdominal cavity. Little of the fast disappearing fin fold remained, when the fin rays of the ventral fin first appeared and the posterior tip of the vertebral column showed a marked upturning (Fig. 16g). Fourteen fin rays could be seen now in the caudal, 4 in the dorsal and seven in the ventral fins. The larvae fed on phytoplankton or small plant material in the aquarium judging from the green occasionally brown colouration of their faeces; however they were fed also on fine plankton caught in Bovine silk mesh, which they took quite avidly making short forward darting movements, while swimming or floating very close to the water surface. Only occasionally did they forage along the bottom. Yellow green colouration appeared dorso-laterally at 17d after hatching (Fig. 16h) indicating the first appearance of chromatophores accompanied by many small melanophores. Ten ventral and eight dorsal fin rays, the vertebrae, and neural and haemal spines were now clearly visible. The fin rays of the caudal fin had up to three joints, which were not apparent in the rays of other fins. The full stomach and intestine (Fig. 16i) indicated they were obtaining food.

The streamlined larva (Fig. 16j) was now 8.2mm in length (Fig. 17). The head darkened as chromatophores and melanophores became more numerous, although few chromatophores appeared ventrally. The fins were now similar to those of an adult fish, except for their colour and the apparent absence of the anterior dorsal fin. Small melanophores soon appeared on the ventral and caudal fins (Fig. 18b). When the caudal fin rays had up to 4 joints, the anterior dorsal fin started to appear and the slightly protruding lower jaw was clearly visible. By 39d (Fig. 18c), the larvae (11.5mm in length), started to become opaque due to the rapid increase in numbers of melanophores and chromatophores, and a marked black spot appeared just posterior to the eye. The abdominal cavity and the outer sheath of the eye now developed an opaque silvery layer, but the gill arches could still be seen. The anterior dorsal fin and its six rays, the last of the fins to appear, was now clearly visible and grew quite rapidly (Fig. 18c-d).

Shortly after this scales started to appear, firstly in the antero-dorsal region, and then rapidly all over the body. The overall pigmentation now intensified quite rapidly and the larva assumed the appearance of a juvenile fish, thus terminating the post-larval stage.

The Juvenile

The two stripes running postero-ventrally from the eye appeared when juveniles were in excess of 45d old (12 to 20mm in length, Fig.18e). In the slowest growing aquarium fish they appeared at about five months (Fig. 17). At 45d eleven to twelve large, almost black patches developed laterally along the body and four smaller spots occurred at the base of the caudal fin (Fig. 18e). The base of the fin rays of the anterior and posterior dorsal fins and the ventral fin had dark markings. The background colour of the body was yellowish black and the ventral region was paler. By 55d (Fig. 18f) the background colour had darkened further, and more black spots had appeared, particularly in the mid-lateral region of the body. Twelve pale yellow patches appeared between the lateral dark patches, above which a number of paler dark spots developed which merged with them in front of the anterior-dorsal fin. Melanophores and yellow chromatophores were present around the mouth, over the snout and between the eyes but were few in number under the chin. At 80d (Fig. 18g) the general markings were similar to the adult fish except for the lack of red pigment spots and the yellow colour of the fins, both of which intensified in adults as the breeding season approached. Fish at this stage were capable of adjusting their background colour to a certain extent as shown in Fig. 18h at 100d old.

Adults

Fish were reared in an aquarium and measured over 2½ years. Rate of growth varied depending on quantity of food supplied (Fig 17. A and B). They bred in aquaria in their third summer at 2 years old when their length varied between 45 and 65mm, when they were fed twice weekly. Pond fish grew more rapidly than aquarium fish (Fig. 17 C and D) and may breed in their first, but certainly in their second year. Young fish in ponds often fed on small gastropods and other small invertebrates.

In wild populations in this study, mature males were recorded at a minimum size of 44.7mm and 0.887g in weight, while mature females were slightly larger 49.0mm and 1.210g in weight. These sizes were similar in aquaria grown fish. It seemed likely that fish could mature and breed at 1 year old in the wild in seasons when food was abundant, but may usually take two years. However in aquaria no fish bred in their first year (Fig. 17). *M. mogurnd*a are reported to spawn at one year old when reared in aquaria (Marherr, 1937).

2 Measurements in mm of recently formed post larvae: eye length 0.44 and height 0.39; lens diameter 0.17; depth of body at anus 0.85 and at mid abdomen 0.93; heart length 0.35 and width 0.24; otic capsule diameter 0.33; swim bladder length 0.52 and height 0.15; and head width 0.89.

The largest *M. adspersa* examined was 121mm total length (from Moggill Creek, Brisbane), and on record is 152mm (from Barron River, Queensland, Boxall *et al.* 2002), but the largest recorded from the inland western population was 99mm from Willow Dam.

Adults in this study were characterised by their dark chocolate background colouration dorsally, fading to a pale fawn or buff ventrally (see Fig. 6a and b). Nine to twelve large dark patches, black to grey in colour, sometimes extending as bars dorsally, occurred mid-laterally along the body. Where patches only occurred, further lighter patches occurred dorsal to these. Between and around these patches numerous white and brick red to red spots were present, the latter being more prominent as breeding approached. The ventral quarter of the body lacked any of these markings. The base of the posterior dorsal, caudal and ventral fins had numerous red spots which were brighter during breeding, and the background colour of these fins was pale yellow, often darker towards their extremities. The anterior dorsal fin had a single row of red spots along its base, and this fin and the pectoral and pelvic fins were very pale yellow. In the male the operculum had three white bands interposed with three or four brown bands which became almost brick red at breeding. The two lower darker bands continued antero-dorsally, the upper one terminating at the postero-ventral edge of the eye and the other at the antero-ventral edge of the eye. The female had similar cheek stripes but the opercular stripes were less clearly marked and generally there were only two pairs. In the male the dorsal region of the head often had dark patches and the anterior region of the cheek was darker than that of the female. The ventral region of the head was pale and similar in colour to the ventral region of the body.

Large adult breeding males had a pronounced bulge on the head above the eyes, which was always absent in females (Fig. 6a and b). The bright colour of breeding males and the shape of the urinogenital papilla helped distinguish sexes. The enlarged papillae tapered to a point and curved downwards in the male (Fig, 6c) whilst in the female it was almost parallel sided and terminated rather abruptly with a ragged distal edge (Fig. 6d). The anus in both sexes was anterior to the urinogenital papilla and was surrounded by lips which were pale pink to salmon in colour, forming a triangle with its apex pointing anteriorly.

Gonad Development and Fecundity

The ovaries, white to yellowish in colour, were divided for most of their length and when ripe, were generally unequal in weight and attained about 18% of the body length. The right lobe usually accounted for up to70% of the total ovary weight. The white to cream coloured testes were very flattened and divided, reaching up to 27% of the body length. The left testis was occasionally slightly longer than the right.

The number of gonad samples taken to check on the gonosomatic index, were limited (Tables 3, 4). However, the mean gonosomatic indices determined from females from ponds and Willow Dam during November, December and early January 1967-68, showed a progressive increase, (2.16, 2.64 and 5.86, Table 3), followed by a decline from mid January to mid February (3.67, 1.54 and 2.13). These data suggest that spawning commenced in late December and was tapering off by early February. The maximum G.S.I. recorded for females was 11.74.

The males had a mean G.S.I. for November, December and early January of 0.85, 0.55 and 1.74 respectively, then falling to 0.72 in mid January, following the pattern seen in females. The maximum G.S.I. recorded for males was 2.16 (Table 4).

Annual fecundity is difficult to determine because they are multiple spawners, and all counts are from numbers of large ova present in the ovaries at one time. Only six specimens were checked for fecundity, egg counts from the ovaries varying considerably during the breeding period from 284 to 1300 (Table 3). Immature or small ova were not counted because they were too difficult to separate and most ovaries only possessed small numbers of these amongst other ovigerous tissue. One ovary contained no large ova. Like some other related gudgeons and gobies, this species was able to breed repeatedly and in fairly rapid succession. This could explain the high variability in egg counts, since later spawnings of an individual in any season may produce fewer ova. It was also noticed on occasions that ovaries were only partly spent since a few large ova remained.

Discussion

A brief summary of a portion of the breeding biology from this work was published by Llewellyn (1971) and Hoese *et al.* (1980). This was the basis of much of the breeding biology information in Merrick and Schmida (1984), Koehn and O'Connor (1990), Morris *et al.* (2001) and in Larson and Hoese (1996); often now wrongly attributed to the latter authors. This information is the complete data from the original study. An extensive summary of the current knowledge of both *M. adspersa* and *M. mogurnda* has been carried out by Pusey *et al.* (2004). However the majority of the information relates to Queensland wild populations where most of the work has been carried out. No comparisons have been made between egg and larval development and much of the breeding biology of the Murray Darling population and the coastal populations. This is particularly important as unpublished electrophoretic studies suggest the Murray Darling population of *M. adspersa* displays considerable genetic divergence from east coast stocks and probably warrants classification as a separate taxon (Wager and Jackson 1993). Thus little data is available on egg and larval development that is known to be from the coastal population to enable full comparisons to be made with the data in this study from the western population.

Diagnostic characters of *M. adspersa* eggs and larvae

The most diagnostic character of *M. adspersa* eggs are the elongate elliptic shape with adhesive discs at one of the narrow ends. A further diagnostic character at least in the

Table 3. Reproductive status of *M. adspersa* females caught at Willow Dam or in ponds at the IFRS* (Inland Fisheries Research Station, Narrandera).**The only GSI determined from preserved ovary weight

Capture date	Locality	Length of fish (mm)	Weight of fish (g)	Ovary weight fresh (g)	Gono-somatic index	Ovary weight preserved (g)	Fecundity (Number of eggs)
23.xi.67	Willow Dam	55.0	1.811	0.038	2.10	-	-
23.xi.67	Willow Dam	55.5	1.946	0.041	2.11	-	-
23.xi.67	Willow Dam	56.0	2.016	0.046	2.28	0.050	1115
Mean	Willow Dam	55.5	1.924	0.042	2.16	-	-
12.xii.67	Willow Dam	49.0	1.210	0.020	1.65	-	-
12.xii.67	Willow Dam	52.1	1.557	0.045	2.89	-	-
12.xii.67	Willow Dam	53.0	1.595	0.040	2.51	0.031	-
12.xii.67	Willow Dam	61.0	2.121	0.044	2.07	-	-
12.xii.67	Willow Dam	61.9	2.265	0.074	3.27	0.053	342
12.xii.67	Willow Dam	62.5	2.392	0.082	3.43	-	-
Mean	Willow Dam	56.6	1.857	0.051	2.64	-	-
8.i.68	Pond 19 IFRS*	49.7	1.213	0.029	2.39	-	-
8.i.68	Pond 19 IFRS	53.5	1.499	0.051	3.40	-	-
8.i.68	Pond 19 IFRS	54.0	1.675	0.053	3.16	-	-
8.i.68	Pond 19 IFRS	59.2	2.100	0.181	8.62	0.160	284
8.i.68	Pond 19 IFRS	65.0	2.734	0.321	11.74	-	1300
Mean	Pond 19 IFRS	56.3	1.844	0.127	5.86	-	-
16.i.68	Pond 18 IFRS	60.0	2.284	0.111	4.86	-	-
16.i.68	Pond 18 IFRS	63.2	2.802	0.042	1.50	-	-
16.i.68	Pond 18 IFRS	66.0	2.974	0.138	4.64	-	-
Mean	Pond 18 IFRS	63.1	2.687	0.097	3.67	-	-
31.i.68	Pond 18 IFRS	65.7	3.005	0.047	1.56	-	-
31.i.68	Pond 18 IFRS	67.7	3.179	0.044	1.38	-	-
31.i.68	Pond 18 IFRS	68.5	3.300	0.060	1.82	-	-
31.i.68	Pond 18 IFRS	70.0	3.519	0.067	1.90	-	-
1.ii.68	Pond 18 IFRS	63.9	2.768	0.035	1.26	-	-
1.ii.68	Pond 18 IFRS	71.0	3.573	0.048	1.34	-	-
Mean	Pond 18 IFRS	67.8	3.224	0.050	1.55	-	-
15.ii.68	Pond 18 IFRS	67.8	3.177	0.061	1.92	-	-
15.ii.68	Pond 18 IFRS	69.0	3.682	0.080	2.17	-	-
15.ii.68	Pond 18 IFRS	72.0	2.652	0.061	2.30	-	-
Mean	Pond 18 IFRS	69.6	3.170	0.067	2.11	-	-
16.i.68	Pond 19 IFRS	60.2	2.714	0.286	10.54	-	-
-	Pond 18 IFRS	94.0	11.160	-**	4.89	0.546	591

Murray Darling population, is the small and often diffuse distribution of oil globules throughout the yolk during most of the stages of egg and larval development.

The post-larvae can be difficult to differentiate from some of the other inland species, particularly those of *Macquaria ambigua* (Golden Perch), *Bidyanus bidyanus* (Silver Perch) and *Leiopotherapon unicolour* (Spangled Perch). In *M. adspersa* the dorsal and ventral lines of melanophores post abdominally (Fig. 18a and b) are the most useful diagnostic characters, together with comparison of the overall body shape, position of the anus, colour and size of the swim bladder and timing of pigmentation in the eyes (see Lake 1967; Llewellyn 1973). In *P. grandiceps* and *H. klunzingeri* the post larvae are much more elongated than those of *M. adspersa*. The characteristics of shape of the gut and the relative position of the anus have been noted as helpful in identifying post larvae of eleven families of larval fishes from Oklahoma (May and Gasaway 1967).

It should be noted that the anterior dorsal fin of *M. adspersa* post larvae was not obvious until 39 days after hatching when it was 11½ mm in length, which may cause confusion in their identity.

Table 4. Reproductive status of *M. adspersa* males caught at Willow Dam or in ponds at the IFRS* (Inland Fisheries Research Station, Narrandera).

Capture date	Locality	Length of fish (mm)	Weight of fish (g)	Testes weight (g)	Gono-somatic index
23.xi.67	Willow Dam	54.0	1.749	0.012	0.69
23.xi.67	Willow Dam	56.0	2.010	0.012	0.60
23.xi.67	Willow Dam	57.0	2.138	0.019	0.89
23.xi.67	Willow Dam	60.0	2.307	0.025	1.08
23.xi.67	Willow Dam	63.0	3.260	0.023	0.71
23.xi.67	Willow Dam	64.0	2.749	0.031	1.13
Mean	Willow Dam	59.0	2.369	0.020	0.85
12.xii.67	Willow Dam	44.7	0.887	0.002	0.23
12.xii.67	Willow Dam	47.3	1.049	0.005	0.48
12.xii.67	Willow Dam	48.6	1.099	0.002	0.18
12.xii.67	Willow Dam	50.2	1.307	0.006	0.46
12.xii.67	Willow Dam	53.0	1.451	0.009	0.62
12.xii.67	Willow Dam	54.0	1.525	0.009	0.59
12.xii.67	Willow Dam	54.4	1.535	0.014	0.91
12.xii.67	Willow Dam	59.1	2.213	0.014	0.63
12.xii.67	Willow Dam	59.3	2.104	0.013	0.62
12.xii.67	Willow Dam	61.0	2.400	0.012	0.50
12.xii.67	Willow Dam	61.0	2.574	0.022	0.85
Mean	Willow Dam	53.0	1.649	0.010	0.55
8.i.68	Pond 19 IFRS*	45.8	0.968	0.010	1.03
8.i.68	Pond 19 IFRS	58.7	2.222	0.045	2.03
8.i.68	Pond 19 IFRS	61.4	2.556	0.045	1.76
8.i.68	Pond 19 IFRS	62.5	2.639	0.057	2.16
Mean	Pond 19 IFRS	57.1	2.096	0.039	1.74
16.i.68	Pond 18 IFRS	59.1	2.289	0.019	0.83
16.i.68	Pond 18 IFRS	59.9	2.248	0.017	0.76
16.i.68	Pond 18 IFRS	61.6	2.497	0.018	0.72
16.i.68	Pond 18 IFRS	62.0	2.541	0.017	0.67
16.i.68	Pond 18 IFRS	64.3	2.953	0.019	0.64
Mean	Pond 18 IFRS	61.4	2.506	0.018	0.72
1.11.68	Pond 18 IFRS	67.2	3.270	0.019	0.58

Comparison of eggs of *M. adspersa* with other native fish of inland NSW.

Breder and Rosen (1966) presented information on breeding of seven species of fish in various genera, including *Mogurnda* sp., in the family Eleotridae. In all cases the eggs were adhesive and most had adhesive discs. Of these descriptions, only the *Mogurnda* and *Carassiops (=Hypseleotris)* genera are represented in inland New South Wales. However a third genus in this family, *Philypnodon,* also occurs in this area. The breeding biology of species in these three genera is very similar. The only other native fish from this region so far described to have an adhesive chorion, but not in the form of discs, are *Maccullochella peelii* (Murray Cod, Lake 1967), *Retropinna semoni* (Australian Smelt, Milward 1965), *Gadopsis marmoratus* (River Blackfish, Jackson 1978) and *Gadopsis bispinosus* (Two-spined Blackfish, Sanger 1990), and *Melanotaenia fluviatilis* (Murray River Rainbow Fish, pers obs.) which have a cluster of long adhesive filaments. However, in these five species, and all other native fish recorded from this region the eggs are spherical (some pelagic, others scattered randomly, and some lay in nests as in the Freshwater Catfish *(Tandanus tandanus))* (Lake 1966, 1967).

Table 5. Comparison between *M. adspersa* and *Philypnodon grandiceps*.

	Mogurnda adspersa	*Philypnodon grandiceps* (Llewellyn in press)
Ova shape	Elliptical	Elongate tear-drop
Ova measurements in mm	1.07-1.33x2.03-3.78	0.69-0.90x1.15-2.17
Ova type	Demersal, adhesive disc, attached	Demersal, adhesive disc, attached
Oil globule	Hundreds very small in egg. Dispersed in larva	Up to 25, coalesced to few at ½egg development. 1 large in egg
Length of egg stage	3d 3h - 8d 8h (20.2-29.0°C)	4d 20h-8d 8h
Prolarva length at hatching	3.44-4.15mm	3.17-4.64mm
Length of prolarva stage	6d 15h (19.0-29.0°C)	3d 12h (19.0-26.2°C)
Post larva length at start	5.30-5.85mm	3.93-4.64mm
Key characters	3 opercular stripes on juvenile fish from 12-20mm 45 days	Dark spot at base of caudal peduncle from mid prolarval stage
Male and female matured	M 44.7mm, F 49.0mm. 1-3year	1year
Largest fish	9.9cm	11.0cm
Fecundity	Up to 1300	Up to 2020
Gonosomatic index Male Female	 Up to 2.15 Up to 11.75	 Up to 0.27 Up to 11.92
Breeding season	December – February.	October - April
Breeding requirements Water temperature °C Food needed	 20.0-29.5 (surf. temp 34.0) Abundant	 18.0-28.0 Abundant
Spawning	Laid in clusters in nest Male guards nest Complex display M & F papillae distinct	Laid in clusters in nest Male guards nest Complex display M & F papillae distinct

Comparison between *M. adspersa* and *P. grandiceps*

The breeding of *M. adspersa* resembles *Philypnodon grandiceps*, the flat headed gudgeon more closely than any other species occurring in inland NSW (Llewellyn 1971; in press.), and a summary of the comparisons for distinction are provided in Table 5. Their breeding displays are very similar and they both can be sexed by their urino-genital papillae during breeding. The tear-drop shaped eggs with up to 25 (approximately six large and 12 small) oil globules during ova development in *P. grandiceps* are quite distinct from the elliptical eggs and small oil globules in *M. adspersa*. At hatching *P. grandiceps* usually possess a single large oil globule at the anterior end of the yolk. Coalescence of oil globules in larvae of *M. adspersa* usually occurs at the termination of the prolarval stage, when the yolk is absorbed and even then the oil globules are usually relatively small.

Breeding season

M. adspersa breeds in the wild between December and February in the Murray Darling system, similar to the southern coastal population but unlike the population in the wet tropics in the north which breeds in October and November (Pusey *et al.* 2004). Flood periods appear to be avoided, as flooding may affect survival of their sedentary adhesive eggs. In the majority of other native fish occurring in the Murray Darling system, breeding is triggered by the spring floods when temperatures are rising and food is abundant (Lake 1967). *Galaxias rostratus* (Murray Jollytail), is an exception, as it spawns in early August prior to these floods. *M. adspersa* appears to prefer sites which are sluggish, slow flowing, have low turbidity, are weedy and lack floods for breeding.

The sampling data (Table 1, Fig. 3) suggest that during October, November and December fish move from the deeper swamp dominated by *Typha* sp., where they are less likely to be caught to the shallower weedier areas dominated by *Vallisneria* sp. Blewett (1929) also inferred that *M. adspersa* moved from deeper water to shallow streams in summer where they were more readily caught. Their movement to shallower, weedier areas is likely to be associated with an increase in available food in these areas where flooding does not occur, eventually giving rise to the onset of breeding. Pusey *et al.* (2004) summarised the limited evidence in support of movement of fish in the coastal populations. In the population south of Tully, Queensland, Whitehead (1985) found that fish moved to deep pools in the dry season, its distribution influenced by the water regime in the creek.

Although seasonal temperature changes also play an important part in influencing the productivity of lentic waters, this study suggests breeding of *M. adspersa* is linked to the abundance of its food, in part brought about by its movement to more productive habitat, rather than specifically to temperature change. Spawning in aquaria was induced between 19.2 and 29.9°C by increasing the food supply for 3-4 weeks.

Breeding habitat, nursery areas and larval survival

The areas where *M. adspersa* were caught and bred were stable water bodies that seldom dried up. Their weedy nature and slow flow provided essential cover, food for adults and larvae and other environmental conditions for a species that has a low fecundity, parental care of the egg cluster, and a need to keep the eggs silt free. These water bodies provided also a suitable substratum for attachment of the eggs and a nursery area for larvae. Similar nursery areas are chosen by *Nannoperca australis* (Llewellyn 1974). In most recorded cases, eggs have been attached to solid objects, but Ashford (1981) and Hansen (1988) recorded them attached to leaves and Freund (1918) to clumps of algae (Table 6, 7). It seems likely this species will avoid rivers with high sediment loads and large water level fluctuations. This breeding strategy is in contrast to that of other fish with high fecundities, such as *Macquaria ambigua* which produces ½ million pelagic eggs and provides no parental care (Lake 1966), or *Leiopotherapon unicolor* which produces up to 113,000 demersal eggs and disperses them randomly in order to minimise the loss from desiccation in drying water bodies (Llewellyn 1973).

All spawnings observed in this study occurred during daylight hours. Visual displays were very elaborate and it is assumed that these displays are most effective in daylight. When fish were observed at night they were resting on the bottom. Hamlyn-Harris (1931) suggested that the ova of this species are laid at night, but he never actually observed them breeding.

Compared with other species, the incubation period (3d 3h to 8d 8h) was long. However egg survival was not compromised, as the egg cluster was guarded by the male throughout. Differences of opinion exist as to whether the male forages for food during the period of egg caring. Funnell (1937) and Blewett (1929) suggested little is eaten, Gale (1914) assumed they fed at night, while in this study they were not seen feeding.

The changing shape and diminishing size of the yolk of late prolarval *M. adspersa* helped to streamline the larva as exogenous feeding commenced. The well developed mouth, pigmented eyes and the neutral buoyancy which occurred when the yolk sac is absorbed, all contribute to the larvae successfully surviving the critical period during the change from endogenous to exogenous feeding. These factors, together with ideal nursery area selection, all contribute to optimum survival of young.

Fecundity

Fecundity of individual *M. adspersa* taken at one point in time was highly variable (Table 3). This could be due to the timing of the sample with respect to stage of development during the rapidly changing repetitive spawning cycles in a single breeding season, and a possible decline in ova production at each spawning as a result of loss in condition of the fish as the breeding season progressed. Hence the number of large countable ova is likely to be highly variable depending whether spawning had just occurred or not. Also partial spawning of mature ova is known to occur, which may cause variation in fecundity counts. Fecundity may vary also annually, based on a change in type or abundance of food (McKay and Mann 1969). Pusey *et al.* (2004) recorded total fecundity for N and SE Queensland populations as 66-1778 and 267-727 respectively compared with 284-1300 for the Murray Darling population in this study. How these figures relate to a total annual fecundity is unclear, but it could vary between 500 and 10,000 ova per female per season.

Although maturity stages in gonad development were examined briefly, the gono-somatic index was the principal method used to follow ovary development. Raja (1966) recommends however the use of both methods simultaneously.

Because of its low fecundity and hence its relatively low potential recruitment rate, it appears that *M. adspersa* is of little value as a forage fish for larger commercial species and would thus have little value in fish farming practices. Nevertheless management measures to conserve its populations in the wild are needed if its perceived population decline is real.

Heart Rate

The heart rate, which varied from 140 to 204 b.p.m. with a mean of 175 b.p.m. at hatching, was considerably faster than recorded for *N. australis* (93 - 115 b.p.m.) and *Edelia vitatta* (112 - 114 b.p.m.) (Llewellyn 1974). The significance of this is questionable because many other variables exist.

Comparison of descriptions of breeding of *M. adspersa* and *M. mogurnda* outlined by other authors

Pusey *et al.* (2004) summarises extensively the current knowledge of *M adspersa* and *M. mogurnda*, but states that details of reproduction in *M. mogurnda* are available in Bishop *et al.*(2001) and are not repeated. This has largely avoided the problem which exists with regard to the literature dealing with reproduction, particularly egg and larval development, of these two species. In most studies, it is not known from where the specimens originate, and thus it is difficult to determine to what species they belong in current taxonomy.

Numerous successful spawnings of *Mogurnda* species have been documented including observations by Gale (1914 and 1918), Freund (1918), Blewett (1929), Hamlyn-Harris (1931), Hansen (1988), Briggs (1998) and Tappin (1997) for *M. adspersa*; Lederer (1935), Funnell

Table 6. Comparison of information reported by authors under the name of *Mogurnda adspersa*. M, male; F, female; RF, Rainbowfish.

Author	Hamlyn-harris 1931	Hansen 1988	Blewett 1929	Gale 1914	Freund 1918	Tappin 1997	Briggs 1998	Llewellyn, this study
Species	*Mogurnda m. adspersa* Identity unsure	*Mogurnda adspersa* Identity unsure	*Mogurnda adspersa* Identity unsure	*Mogurnda adspersa* Identity unsure	*Mogurnda adspersa* Identity unsure	*Mogurnda adspersa*	*Mogurnda adspersa* Inverell population	*Mogurnda adspersa*
Comment	No location. Some doubt on species	Collection site not stated. From E coast and Murray Darling 2 species	Probably collected lower Murray	Collection site not stated	America, from H.E.Finckh. RZS site collected, not stated	No collection site	Collected Deadman's Creek 20km W of Tenterfield	Collected Barren Box, Near Griffith, NSW
Egg shape	-	-	elongate	-	elongate	oblong	-	Elliptical
Egg dimension mm	-	-	-	36h to elongate	-	-	-	1.07-1.33 by 2.03-3.78
Egg type	adhesive	adhesive	adhesive	Hair like filament Gelatinous base	Light brown in colour. Adhesive	Sticky base	Adhesive	Demersal, transparent, adhesive disc
Oil globule	-	-	-	Globule of <u>air</u> on yoke	-	-	-	Small and numerous
Length of egg stage - days/hours	5-8d (6d)	7-8d	14d cold snap died, 3d	9d	5-6d (at 26.7°C)	5-9d	6-9d (20°C)	3d 3h -8d 8h at 20.2 -29.0°C
Prolarva length at hatching in mm	4-5	-	-	-	-	-	-	3.44-4.15
Prolarva stage in days/hours	-	6d	1.5d	(Guarded by M for 24 hours)	-	-	1.5d	6d 15h at 19.0-29.0°C
Key characters of fish	-	-	Brilliant colour when spawning	-	Bright colours when spawning	-	-	Brighter colours when spawning
Mature M & F in mm	115	-	76	126. bred at 3 years	65+	-	-	>M 44.7 and F 49.0 Bred at 2-3 years
Longest fish cm	-	15	-	-	-	10	11	9.9
Number of eggs laid per spawning	100 to 200 per spawning	Approx 300	100-200	-	Approx 100	300-1200	30-300+	774 one count
Breeding season	October -January	Longer days	Spring & summer	November to March	-	Dec-Feb	-	December to February in the wild

Author	Hamlyn-harris 1931	Hansen 1988	Blewett 1929	Gale 1914	Freund 1918	Tappin 1997	Briggs 1998	Llewellyn, this study
Breed – Temp. °C	-	(Tolerates 19-34)	18.3-27.8	26.7	26.7	Above 20°C	Above 20°C	20. 0-29.9, 34.0°C Surf. Temp.
Food	Abundant	Abundant	Fed daily	-	-	Adequate	-	at least once daily
No. fish in aquarium	2 in 75 L	2+ in 60 L	2 in 55 L	2 in 38 L	-	Adequate space	4-6 (120cm + RF)	3-11 in 90 L aquaria
Spawning time	Not seen	-	6.50am daytime	morning	morning	-	-	Daytime
Spawning frequency	6 batches in 45 days	Laid in a batch	-	10 batches November - March	2 batches in 6 days	-	-	11 fish spawned 12 batches, 12 Oct - 6 Nov 69
Spawning site	Glass	Solid objects, leaves	Stones	Glass	Glass, algae	Solid objects	Firm surfaces	Hard objects
Start larval feeding	-	-	-	-	-	When hatched	1-1.5d	6d 15h after hatching
Distribution	-	-	-	-	-	Murray Darling + NE coast		Murray Darling
Time of eye pigment	4d ?	-	-	3d first visible	2d eye pigment	3d	-	3.5d after fertilisation
Growth d = days, m = months	-	42 d 10mm 7 m 50mm	-	1 year 40-50mm	10d 6.5mm	25mm in 2m Red spots in 4m 45-50mm in 10m	Varies sorting needed	20mm 4m) 34mm 12m) 50mm 24m) in aquaria
Papilla	-	M pointed	-	-	-	-	-	M pointed. F blunt.
Sex differences	M brighter	M more colour, Forehead bulge, pointed papilla	M blunter forehead	M lighter in colour	-	-	-	Large M with forehead bulge. Papillae M pointed, F blunt. M most colourful.
General	-	-	Migrate from deep water to stream in summer	Number of sterile eggs increased with each brood	-	pH 6.8-7.5	pH 6.8-7.8	Migrate from deep water to stream in summer. Ceased egg care at night.
Display/ care	Elaborate display M cared for eggs	Elaborate display M cared for eggs	Elaborate display M cared for eggs	M cared for eggs	M cared for eggs	Prepares site. M cares for eggs	Elaborate displays. M cares for eggs	Elaborate display M cared for eggs

Table 7. Comparison of information reported by authors under the name of *Mogurnda mogurnda*. M, male; F, female; N, north; Q , Queensland; pict, dimensions estimated from drawing.

Author	Azuma 1984	Marherr 1937	Funnell 1937	Schiessl 1937	Miller 1970	Ashford 1981	Young 1987	Lederer 1935
Species	*M. mogurnda* Identity unsure	*M. mogurnda* Identity unsure	*M. mogurnda* Identity unsure	*M. mogurnda* Identity unsure	*M. mogurnda* Identity unsure	*M. mogurnda* Identity unsure	*M. mogurnda* Identity unsure	*M. mogurnda* Identity unsure
Comment	Japan – Imported. No location.	Bought as juvenile in Germany 2 species exist. ?	Germany, confusion over species	Very short note	Caught in Q waterholes No location	N.Australia, Q & N NSW. No location	Bought Adelaide. No location Several species exist	German (not translated)
Egg shape	Oblong, oval	Elliptical	-	-	-	-	Elongate	Elliptical
Egg dimensions mm	2.1 long	2.70 (2.6x0.9 pict.)	-	-	-	-	3.0 long	-
Egg type	Milky white	Adhesive disc demersal, clear	Adhesive thread demersal	Adhesive	Adhesive thread Light brownish	Attached	Attached	-
Oil globule	-	-	-	-	-	-	-	-
Length of egg stage days	7 at 27.2°C	9-10½	4-5	10-12	-	Few days ?	5-6	13 at 21-23°C
Prolarva length at hatching in mm	10	4.5, (5.0mm at 30h)	6 approx	-	-	-	-	-
Prolarva stage in days	-	8	-	-	-	-	(M cares for young)	-
Key characters of fish	4 months spots 9 months coloured	-	-	-	-	-	-	-
Mature M & F in mm	65	-	M 90, F 100 Yellow fins brighten	-	-	-	M 100, F 100	-
Longest fish cm	20	20	10, reports up to 20	15 in aquaria	-	17.5	10	-
Number of eggs laid per spawning	300	350-500. Up to 1000	100	-	-	-	-	-
Breeding season	-	-	-	-	-	-	-	-
Breed - Temp °C	-	21-26	22.2- 26.7	-	22.2-25.2	-	24.0	-
- Food	Abundant	Abundant	Abundant earthworm	Earthworms	-	-	Abundant	-
- No. fish in aquaria	2 to 42 L	2M, 5F to 45 L	10 to 36 L	4 M. 4 F in 204L.	-	6 in 86 L	2 in 90cm aquarium	-
Spawning time	-	day	afternoon	-	-	-	-	-
Spawning frequency	6 batches in 15 days	-	1 week apart, repetitive spawning	10 batches Nov. to March	-	3 batches in 14 days	3 batches in 20 days	-

Author	Azuma 1984	Marherr 1937	Funnell 1937	Schiessl 1937	Miller 1970	Ashford 1981	Young 1987	Lederer 1935
Spawning site	Stones, glass	Laid in batch, stones	Hard objects, glass	Glass	Hard surface, glass	Hard surface, leaf	On rock	-
Start larval feeding	At hatching	At 8 days	12 hours	-	-	-	At Hatching	-
Distribution	Central & N. Australia	-	-	-	-	-	-	-
Time of eye pigment	2 days at 27.2°C	5 days	3-4 days	-	-	-	Approx. 5 days	-
Growth d=days m=months	2 m 25mm 4 m spots 6 m full colour	15 d 10mm 20 d 13mm 35 d 20-25mm 12 m 9-12cm	-	-	-	-	10mm black spots present	-
Papilla	-	F oval M pointed	-	-	-	-	-	F blunt M pointed
Sex differences	-	Papilla	Males more vivid	-	-	-	M bulbous head	Papilla
General	-	Eggs sketched	-	-	-	-	-	Eggs sketched
Display/care	Elaborate display M cares for eggs	M cares for eggs	Elaborate display M cares for eggs	M cares for eggs	M cares for eggs	M cares for eggs	Elaborate display M cares for eggs	-

(1937), Marherr (1937), Schiessl (1937), Miller (1970), Ashford (1981), Azuma (1984) and Young (1987) for *M. mogurnda*, and T. Johnson (personal communication) for an unknown species of *Mogurnda*. Breder and Rosen (1966) summarised some of the findings of these authors. Marherr (1937) and Lederer (1935) were the only authors to give a brief description and some brief sketches of the embryological stages of *M. mogurnda*. Since most of these accounts did not identify the locality where the specimens were collected, many descriptions could have been related to newly described species of the *Mogurnda* genus. Many authors expressed confusion over the identity of their fish. Also because of the remaining uncertainty with regard to the various *M. adspersa* stocks it is only pertinent to make comparisons with the Murray Darling stock used in this study. The value of these comparisons is however limited.

Tables 6 and 7 summarise the descriptions of breeding provided by other authors for *M. adspersa* and *M. mogurnda* respectively. "Comments" in these Tables with respect to collection are my own comments. The breeding information available provides little to differentiate between the two species, which is often further complicated by the lack of close prolonged and magnified observation of eggs and spawning. Two factors do however stand out, firstly the maximum size observed in the Murray Darling population for *M. adspersa* of 99mm in this study and the maximum size reported for *M. mogurnda* (Funnel 1937; Marherr 1937; Azumo 1984) of 200mm. The maximum size of fish in the east coast populations of *M. adspersa* is usually 100mm with one record from the Barron River of 152mm (Pusey *et al*. 2004). Secondly aquarium experiments in this study indicated fish bred at two or three year old as was also found by Gale (1914, 1918). In comparison, some *M. mogurnda* aquaria studies showed fish breeding at one year old. This needs confirmation in wild stocks.

As in this study Blewett (1929), Hamlyn-Harris (1931), Funnell (1937), Marherr (1937), Azumo (1984), Young (1987) and Hansen (1988) emphasize the need for conditioning of fish, and an abundant, constant source of food, preferably twice daily for inducing spawning. Food items reported to be used for conditioning of *Mogurnda* spp. in aquaria included earthworms, young yabbies, shrimps, insects (mosquito larvae (*Culex* sp.) and fly larvae), scraped beef, tadpoles, *Daphnia*, *Gambusia holbrooki* (Mosquito Fish), other small fish, *Cyclops* and snails. Food seems to be an important trigger for all *Mogurnda* species.

The temperature at which spawning was recorded by other authors for *M. adspersa* and *M. mogurnda* was similar but varied between 18.3 and 27.8°C as compared with 20.0 – 29.9°C (34.0°C surface water temperature) in this study.

Most authors reported intensifying of colours, particularly in males, as breeding approached; however, Funnel (1937) stated that the yellow in the fins was the only colour that brightens. Blewett (1929) was the only author to comment on the blunter head of the male, but a number of authors mentioned the bulge on the head of some adult males as was the case in this study. Opinions differed amongst authors as to whether adults could be sexed by the shape of the dorsal fin; differences of this nature were

not observed in *M. adspersa* during the present study. Lederer 1935 and Marherr (1937) for *M. mogurnda* and Hansen (1988) for *M. adspersa* reported differences in the urino-genital papilla at spawning as found in this study.

Blewett (1929), Hamlyn-Harris (1931), Funnel (1937), Young (1987), Hansen (1988) and Briggs (1998) describe similar spawning displays as found in this study; namely, head to tail positioning, rolling and body quivering with fins erect, occasional expanding of gill covers, mouth prodding, jaw snapping and cleaning and preparation of spawning sites which were comprised of stones, slate, glass sides of aquaria, leaves (Hansen 1988, Ashford 1981) and a clump of algae (Freund 1918).

In all cases in *Mogurnda* sp. the adult male was observed to fan and guard the egg clusters. Only Gale (1914) stated that the larvae were guarded by the male for approximately 24 hours after hatching, most other authors inferred that care of the cluster of ova terminated at hatching, when the male immediately started to seek out another breeding female. Hamlyn-Harris (1931) found that the adult male ceased care of the eggs at night as was found in this study, and he also stated that many ova were lost because of female cannibalism. This occasionally occurred in this study, particularly when the male was small and the female large, and the male therefore was unable to protect the ova on completion of spawning.

Seven hundred and seventy four ova were laid in one spawning in this study, while Marherr (1937) and Tappin (1997) reported clusters of eggs up to around a 1000 in number. Other authors reported considerably less for both species of *Mogurnda*, between 100 and 300 for each spawning, while Pusey *et al.* (2004) indicated that total fecundity in coastal Queensland populations of *M. adspersus* varied from 66 and 1778. Blewett (1929) observed that 30 ova were fertilised at each attempt by the male, but Gale (1914) and Marherr (1937) stated that 8 and 3 - 10 respectively were usual. At one spawning in this study between 1 and 30 ova were laid for each fertilisation attempt, numbers being highly variable (Fig. 6).

Miller (1970) reported eggs of *M. mogurnda* to be light brownish and Azuma (1984) to be milky white, somewhat unlike that found for *M. adspersa.* Gale (1914), Funnel (1937) and Miller (1970) report that the eggs in *M. mogurnda* were attached by a single thread like filament allowing them to waive, which is also different from the filamentous disc found during this study. It is possible that these are differences between *M. mogurnda* and *M. adspersa* but confirmation and further details are needed.

Gale (1914) stated that *M. adspersa* took 36 hours for the eggs to elongate (the process was around 4hr in observations reported here, Fig. 9), and he also refers to a globule of air on the yolk. This could be a large oil globule but is unlike any of the developmental stages reported in this study, since the oil globules were generally small and dispersed throughout the yolk. The population being described by Gale could well be different from the Murray Darling population.

In this study most eggs attended by a male hatched in 4 days, but varied between 3-7days. Unattended eggs (e.g. in petri dishes) took up to 8 days 8 hours to hatch at 20 – 29°C. Blewett (1929) indicated that all eggs of *M. adspersa* died when hatching took 12 days during a cold period. According to other authors the times taken for eggs to hatch varied from 3 to 14 days, but no consistency of results could be determined for *M. adspersa* and/or *M. mogurnda* (Table 6 and 7). Marherr (1937) reported the longest hatching times for *M. mogurnda* of 8 - 10½ days, while temperatures varied from 18 – 26°C. The sizes of eggs 0.9 x 2.7mm and lengths of larvae at hatching 4.5mm and 5mm at 30 hours Marherr (1937) were similar to this study. Thereafter, however, Marherr reported a more rapid growth of fish being 10mm at 15 days and 12 - 13mm at 20 days, than in this study (8.2mm at 29 days).

Both Gale (1914) and Hamlyn-Harris (1931) recorded the breeding frequency of a pair of *M. adspersa*. Fish laid 10 batches over 105 days (on day 1,33,42,53,63,76 +4), involving the male in 90 days of brood care (Gale 1915), and 6 batches over 45 days (on day 1,10,18,21,32,45) (Hamlyn-Harris 1931). These observations were similar to that found in this study and that found by most other authors. Authors indicated that once exogenous feeding of larvae commenced, food such as plankton, powdered milk, powdered egg, brine shrimp and chopped enchytraeid worms were found to be suitable.

In this study, aquarium *M. adspersa* reached 30-40mm in 12 months (Fig. 17) compared with 40-50mm in 12 months found by Gale (1914). These rates of growth varied substantially from that reported by Marherr (1937) for *M. mogurnda* where they reached 90 - 120mm in aquaria in that period. Although Marherr (1937) hinted that there was some doubt existing as to the *Mogurnda* sp. used, it seems likely that the vastly differing growth rates could be due to them being different species (*M. mogurnda* and *M. adspersa*) or possibly being kept in differing conditions with different food supplies; further confirmation on this is needed.

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References

Allen, G.R. and Jenkins A.P. 1999. A review of the Australian freshwater gudgeons, genus *Mogurnda* (Eleotridae), with descriptions of three new species. *Journal of Ichthyology and Aquatic Biology.* **3(4):**141-156.

Allen, G.R., Midgley, S.H. and Allen, M. 2002. *Field Guide to the Freshwater Fishes of Australia.* Western Australian Museum, Perth.

Ashford, R. 1981. The Persian Carpet *Mogurnda mogurnda*. *Fishtales, Magazine of Eastern Districts Aquarium Society, Ringwood Victoria 3134, Australia.* **12(10)** Oct. p5.

Azuma, H. 1984. Spawning the Purple Gudgeon. (Translated by K. Mason). *Tropical Fish Hobbyist.* **32(10)**:40-48.

Belsare, D.K. 1962. Seasonal changes in the ovary of *Ophicephalus punctatus* Block. *Indian Journal of Fisheries***. 9(1):** 140-56.

Blackett, R. F. 1968. Spawning behaviour, fecundity and early life history of anadromous dolly varden, *Salvelinus malma* (Walbaum) in south-eastern Alaska. *Alaska Department Fish and Game Research Report.* **6**:1-85.

Blewett, C. 1929. Habits of some Australian freshwater fishes. *South Australian Nat.* **10(2)**:21-9.

Bodola, A. 1964. Life history of the gizzard shad *Dorosoma cepedianum* (Le Sueur), in Western Lake Erie. *Fishery Bulletin. Fisheries and Wildlife Service. U.S.* **65**:391-425.

Boxall, G.D, Sanberg, J.J. and Kroon, F.J. (2002). Population structure, movement and habitat preferences of the purple spotted-gudgeon *Mogurnda adspersa. Marine and Freshwater Research***. 53**:909-917.

Breder, C. M. (Jr.) and Rosen, D. E. 1966. *Modes of Reproduction in Fishes.* Natural History Press, Garden City, New York. 522-3.

Briggs, G. 1998. Murray-Darling *Mogurnda adspersa*. *Fishes of Sahul.* **12(1):**553-556.

Castelnau, F.L. 1878. On some new Australian (chiefly) freshwater fishes. *Procceedings of the Linnaean Society of New South Wales.* **31**:142.

Devillers, C. 1961. Structural and dynamic aspects of the development of the teleostean egg. *Advanced. Morphogen*. **1** (Ch 1x):379-428.

Edsal, A.T. 1970. The effects of temperature on the rate of development and survival of alewife eggs and larvae. *Transactions of the American Fisheries Society.* **99**:376-80.

Freund, E. O. 1918. Notes on *Krefftius adspersus*. *Aquatic Life*. 33-4.

Funnell, B. 1937(Oct). *Mogurnda mogurnda* (Richardson). *The Aquarium.* **6**:106-8.

Gale, A. 1914. Notes on the breeding habits of the Purple Striped Gudgeon. *Australian Zoologist.* **1**:25-6.

Gale, A. 1918. Breeding habits of *Krefftius adspersus*, the Purple-striped Gudgeon. *Aquatic Life*. **Pt 3:**164. (Reprinted from Australian Zoologist **1(1):**25-26. 1914).

Greenwood, P. H., Rosen, D. E., Weitzman, S. H., and Myers, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131**(4):34-455.

Hamlyn-Harris, R. 1931. A further contribution to the breeding habits of *Mogurnda (Mogurnda) adspersa* Castelnau. The trout gudgeon. *Australian. Zoologist.* **7**(1):55-8

Hansen, B. 1988. The Purple-spotted Gudgeon – *Mogurnda adspersa*. *Fishes of Sahul.* **5(1):**200-202.

Hoese, D.F., Larson, H.K. and Llewellyn, L.C. 1980. Family Eleotridae – Gudgeons. Pp. 169-185. In *Field Guide to the Freshwater Fishes of South Eastern Australia*. Edited by R.M. McDowall. Reed: Sydney.

Hubbs, C. L. 1943. Terminology of early stages of fishes. *Copeia.* **1943 (4)**:260.

Jackson, P.D. 1978. Spawning and early development of the River Blackfish, *Gadopsis marmoratus* Richardson (Gadopsiformes:Gadopsidae) in the McKenzie River Victoria. *Australian Journal of Marine and Freshwater Research***. 29(3):** 293-298.

Koehn, J.D. and O'Connor. W.G. 1990. *Biological information for management of native freshwater fish of Victoria.* Department of Conservation and Environment, Freshwater Fish management Branch. Government Printer, Melbourne.

Konstantinov, K. G. 1957. A comparative analysis of the morphology and biology of the perch (*Perca fluviatilis*), the European pike perch (*Lucioperca lucioperca*), and the Volga pike perch (*Lucioperca volgensis*) at different stages of development. *Trudy Inst. Morf. Zhivot.* **16**:181-202 (in Russian).

Kuntz. A. and Radcliffe, L. 1915-16. Notes on the embryology and larval development of twelve teleostean fishes. *Bulletin of the Bureau of Fisheries, Washington.* **35**:89-134.

Lagler, K.F. 1956. *Freshwater Fishery Biology.* Brown, Dubuque.

Lagler, K.F., Bardach. J. E. and Miller, R. R. 1967. *Ichthyology.* John Wiley, New York.

Lake, J.S. 1966. Freshwater fish of the Murray-Darling River System. *New South Wales State Fisheries Research Bulletin.* **7**: 1-48.

Lake, J.S. 1967. Rearing experiments with five species of Australian freshwater fishes, I and II. *Australian Journal of Marine and Freshwater Research.* **18**:137-73.

Lake, J.S. 1971. *Freshwater Fishes and Rivers of Australia.* Nelson, Sydney and Melbourne.

Lake, J.S. 1978. *Australian Freshwater Fishes*. Thomas Nelson Australia: Melbourne.

Larson, H.K. and Hoese, D.F. 1996. *Family Gobiidae, subfamilies Eleotridae and Butinae, Gudgeons,* In *Freshwater Fishes of South-eastern Australia,* edited by R. McDowall. Reed Books: Chatswood.

Lederer, G. 1935. Haltung und Zucht der australischen Forellen = Regenbogen = oder. Tupfelgrundel (*Mogurnda mogurnda*). *Wochenfchrift fur Aquarien und Terrarienkunde* **39** (24 Sept.1935) 609-611.

Lintermans, M. 2003. *Pilot Sustainable Rivers Audit- Fish Technical Report* (Draft). Murray-Darling Basin Commission. Canberra.

Llewellyn, L.C. 1971. Breeding studies on the freshwater forage fish of the Murray-Darling river system. *Fisherman, State Fisheries New South Wales.* **3**(13):1-12.

Llewellyn, L.C. 1973. Spawning, development and temperature tolerance of the Spangled Perch, *Madigania unicolor* (Gunther), from inland waters in Australia. *Australian Journal of Marine and Freshwater Research*. **24**:73-94.

Llewellyn, L.C. 1974. Spawning, development and distribution of the Southern Pigmy Perch *Nannoperca australis australis* Gunther from inland waters in eastern Australia. *Australian Journal of Marine and Freshwater Research.* **25**:121-49.

Llewellyn, L.C. in press. Spawning and development of the Flat-headed Gudgeon *Philypnodon grandiceps* (Krefft, 1864) (Eleotridae) from freshwater areas of New South Wales. (*Australian Zoologist* In press).

Mackay, N.J. 1973. Histological changes in the ovaries of the Golden Perch *(Plectroplites ambiguus*) associated with the reproductive cycle. *Australian Journal of Marine and Freshwater Research.* **24**:95-101.

Manner, H.W. 1964. *Elements of Comparative Vertebrate Embryology*. The Macmillan Company, New York.

Marherr, A. 1937(Sept). Die australische tupfelgrundel, *Mogurnda mogurnda* Richardson. *Blatter fur aquarien und terrarienkunde Natur U. Haus.* **No. (9)48**:189-92.

May, E.B. and Gasaway, C.R. 1967. A preliminary key to the identification of larval fishes of Oklahoma, with particular reference to Canton Reservoir including a selected bibliography. *Bulletin of the Oklahoma Fisheries Research Laboratory.* **No. 5,** Contribution (164):1-42.

McKay, I. and Mann, K.H. 1969. Fecundity of two cyprinid fishes in the River Thames, Reading, England. *Journal of the Fisheries Research Board of Canada.* **26**:2795-805.

Merrick, J.R. and Schmida, G.E. 1984. *Australian Freshwater Fishes, Biology and Management.* Griffin Press: Netley SA.

Miller, S. 1970. *Mogurnda mogurnda*. The Purple Spotted Gudgeon. *The Aquarium Society of New South Wales.* **20**(5):4-5.

Milward, N. 1965. Development of the eggs and early larvae of the Australian smelt, *Retropinna semoni* (Weber). *Proceedings of the Linnaean Society of New South Wales.* **90**(2):218-21.

Morris, S.A., Pollard, D.A., Gehrke, P.C. and Pogonoski, J.J. 2001. Threatened and potentially threatened freshwater fishes of coastal New South Wales and the Murray Darling Basin. *NSW Fisheries Final Report Series* **No. 33**.

Needham, J. 1942. *Biochemistry and Morphogenesis* p. 787. Cambridge University Press, London and New York.

Nikolsky, G.V. 1963. *The Ecology of Fishes.* Academic Press, London and New York.

NSW Fisheries, 2004. http://fishfiles.fisheries.nsw.gov.au

Piavis, G.W. 1961. Embryological stages in the sea lamprey and effects of temperature on development. *Fishery Bulletin. Fisheries Wildlife Service. U.S.* **61**:111-45.

Pusey, B.J., Kennard, M.J. and Arthington, A.H. 2004. *Freshwater fishes of north-eastern Australia.* CSIRO Publishing, Collingwood.

Raadik, T.A. and Harrington, D.J. 1996. *An assessment of the significance of the fish and Decapod crustacea of Cardross Lakes (Main Lakes), Mildura, with special reference to the southern purple-spotted gudgeon.* Freshwater Ecology Section. (DCNR) Report.

Raja, B.T.A. 1966. On the maturity stages of Indian oil sardine, *Sardinella longiceps* Val., with notes on atretic follicles in advanced ovaries. *Indian Journal of Fisheries.* **13(1 and 2)**:27-47.

Richardson, J. 1844. Ichthyology. *Voy. Erebus and Terror Fishes*, **V 2 (2).** p.4, p1ate.2, figs. 1-2.

Sanger, A.C. 1980. Life history of *Gadopsis bispinosus* in King Parrot Creek Victoria. *Proceedings of the Royal Society of Victoria.* **102.**

Schiessl, ?. 1937(March). *Mogurnda mogurnda* (Comments). *The Aquarium* **5**(2):236.

Steindachner, F. 1866. Zur fischfauna von Port Jackson in Australien. *Sitzb. Akad. Wiss. Wein.* **53**:452.

Tappin, A.R. 1997. *Mogurnda adspersa* – the Purple-spotted Gudgeon. *ANGFA Bulletin* **No. 32, August**.

Toetz, D.W. 1966. The change from endogenous to exogenous sources of energy in bluegill sunfish larvae. *Investigations, Indiana Lakes and Streams.* **7(4).**

Wager, R. and Jackson, P. 1993. *The action plan for Australian freshwater fish.* Australian Nature Conservation Agency. Endangered Species Program. Project **Number 147**.

Whitehead, M.D. 1985. *Ecology of the Purple-spotted Gudgeon,* Mogurnda adspersa *(Castelnau) (PISCES – Eleotridae), in a tropical upland rainforest stream.* B. Sc. Thesis. James Cook University, Queensland

Whitley, G.P. 1972. Rains of fishes in Australia. *Australian Natural History.* **17**(5):154-60.

Williams, N.J. 1972. *On the Ontogeny of Behaviour of the Cichlid Fish* Cichlasoma nigrofasciatum *(Gunther)*. Rijksuniversiteit te Groningen. Thesis.

Young, M. 1987. A tank breeding of *Mogurnda mogurnda*. *Fishes of Sahul.* **4(3):**174-177.

Zietz, A.N.C. 1896. Pisces Reports. *Horn Scientific Expedition. Central Australia.* **2**:179.

Zietz, A.N.C. 1902. List of the edible fish of the lower Murray. *Transactions of the Royal Society of South Australia*. **26**(2):p.267.

APPENDIX I

Site A where most of small fish studies were carried out. Willow Dam is above weir and Barren Box swamp starts about 100m downstream. This channel is fairly uniform in depth and shallow (approx 40cm) with much *Vallisneria* sp. and other filamentous algae

APPENDIX I

Site B where most of small fish studies were carried out. Second (of three) weirs with Willow Dam above weir and Barren Box swamp starting about 100m downstream. The channel at this weir is a fairly uneven depth (up to 1.8m), with little weed and often a more rapid flow than in other channel pictured. The third channel (not pictured) is very similar to this channel.

Mogurnda adspersa Male

Mogurnda adspersa Female